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The effect of interannual variation in growth and condition on haddock recruitment

C. Tara Marshall and Kenneth T. Frank

Abstract: The relationship between recruitment and spawner biomass assumes that estimates of spawner biomass are proportional to total egg production by the stock. The validity of this assumption is in question for long-lived gadoid stocks; however, estimating total egg production independently of spawner biomass is seldom feasible. An alternative approach is to examine correlations between recruitment and variables likely to be proxies for total egg production by the stock. This indirect approach was used for haddock on the Scotian Shelf. Indices of growth (mean length at age-4) and condition (weight at 50 cm) were used as proxies for the reproductive potential of individual spawners. Both variables were positively correlated with recruitment over a 3-decade period (1964–1995). During the same time period, there was no relationship between recruitment and spawner biomass estimated by Virtual Population Analysis (VPA). This is further evidence that VPA-based spawner biomass is a poor index of the true reproductive potential of the stock. The results highlight the need to develop more accurate/precise measures of total egg production for use in recruitment research.

Résumé : La relation entre le recrutement et la biomasse des géniteurs s'appuie sur la prémisse selon laquelle les estimations de la biomasse des géniteurs sont proportionnelles à la production totale d'oeufs par le stock. La validité de cette hypothèse est remise en question pour les stocks de gadoïdes à longue durée de vie. Toutefois, il est rarement possible d'estimer la production totale d'oeufs sans tenir compte de la biomasse des géniteurs. Une autre façon de procéder consiste à examiner les corrélations entre le recrutement et les variables considérées comme des approximations de la production totale d'oeufs par le stock. Cette approche indirecte a été appliquée au stock d'aiglefin de la plate-forme néo-écossaise. Des indices de la croissance (longueur moyenne à l'âge de 4 ans) et de la condition (poids à 50 cm) ont été utilisés comme approximations du potentiel reproducteur des géniteurs. Une corrélation positive entre ces variables et le recrutement a été observée sur une période de plus de 30 ans (1964–1995). Durant cette même période, aucune corrélation n'a été observée entre le recrutement et la biomasse des géniteurs estimée par analyse des populations virtuelles. Ces résultats démontrent une fois de plus que l'estimation de la biomasse des géniteurs par analyse des populations virtuelles ne reflète pas fidèlement le potentiel reproducteur d'un stock. Ils font également ressortir la nécessité d'élaborer des instruments de mesure plus justes et plus précis de la production totale d'oeufs à des fins d'utilisation dans le cadre de recherches sur le recrutement.

[Traduit par la Rédaction]

Introduction

In the field of fish population dynamics the most common method of assessing the relationship between the reproductive potential of a stock and the resultant progeny has been to use theoretical models relating spawner biomass to recruitment. This approach assumes that spawner biomass is linearly related to total egg production by the stock. A recent test of this assumption for northeast Arctic (NEA) cod (*Gadus morhua*) revealed that the relationship between total egg production and spawner biomass is non-linear with non-constant variance (Marshall et al. 1998). Furthermore, the magnitude of variation in total egg production was closer to that observed in recruitment (≈100-fold) and the relationship between the two variables approached the origin. The corresponding lack of a relationship between recruitment and estimates of spawner biomass derived from Virtual Population Analysis (VPA) suggests that the latter is a poor measure of the true reproductive potential of the NEA cod stock. The far-reaching implications of this conclusion necessitates that it be investigated for other stocks.

Quantifying total egg production (or abundance) independently of the VPA requires highly specialized databases. For example, total egg production for NEA cod was estimated using acoustic estimates of the total abundance of spawners, demographic information describing the size, sex, and maturity composition of the stock, and year-specific fecundity–length relationships (Marshall et al. 1998). Such

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Table 1. Sampling dates (day/month) for bottom trawl surveys of NAFO Division 4X.

Year	Spring	Summer	Fall
1963	—	—	21/11–23/11
1964	—	—	22/11–22/11
1965	—	—	14/10–15/10
1966	—	—	18/10–20/10
1967	—	—	13/11–15/11
1968	—	—	06/11–07/11
1969	—	—	15/11–17/11
1970	20/03–21/03	07/07–16/07	08/11–13/11
1971	27/03–30/03	30/06–08/07	06/11–12/11
1972	10/03–10/03	25/06–01/07	08/11–14/11
1973	—	10/07–19/07	11/11–15/11
1974	09/03–10/03	09/07–23/07	02/11–03/11
1975	17/02–21/02	15/07–24/07	08/11–13/11
1976	21/02–27/02	13/07–19/07	15/11–15/11
1977	25/03–30/03	10/07–16/07	03/11–05/11
1978	17/03–18/03	10/07–13/07	11/11–12/11
1979	05/03–11/03	06/07–13/07	27/10–28/10
1980	20/03–26/03	07/07–14/07	31/10–01/11
1981	12/03–16/03	06/07–12/07	27/10–05/11
1982	16/03–24/03	10/07–18/07	25/10–27/10
1983	07/04–14/04	07/07–14/07	02/11–03/11
1984	17/03–26/03	10/07–20/07	21/10–22/10
1985	01/03–06/03	04/07–10/07	01/11–02/11
1986	—	08/07–14/07	30/10–31/10
1987	—	29/06–09/07	—
1988	—	04/07–11/07	—
1989	—	05/07–13/07	—
1990	—	04/07–12/07	—
1991	—	04/07–11/07	—
1992	—	22/06–05/07	—
1993	—	05/07–16/07	—
1994	—	04/07–15/07	—
1995	—	25/06–07/07	—

Note: A dash indicates that a survey was not conducted that year. The spring and summer surveys were conducted by the Canadian Department of Fisheries and Oceans and the fall survey was conducted by the U.S. National Marine Fisheries Service.

detailed information describing the abundance and reproductive potential of individual spawners is lacking for many species. Field-based estimates of total egg abundance from synoptic-scale surveys could also be used to test the proportionality assumption. With the exception of stocks assessed using the egg production method (and therefore lacking the corresponding VPA estimates of spawner biomass), field-based estimates of total egg abundance are usually available for only a small number of years. This severely limits their utility for testing the proportionality assumption.

As a practical alternative, interannual variability in reproductive potential can be assessed using variables assumed to be proxies for the reproductive potential of individual spawners and (or) total egg production by the stock. For example, the Shannon diversity index has been used to describe interannual variation in the number and proportional representation of different age classes comprising the Icelandic cod stock (Marteinsdottir and Thorarinsson 1998). A positive correlation was observed between age diversity and recruitment to age-3 (see fig. 3b in Marteinsdottir and Thorarinsson 1998); higher recruitment resulted when the spawning stock had a higher number and (or) proportion of older, larger cod. This suggests that recruitment is influenced by the higher reproductive potential of older cod, an interpretation supported by recent research demonstrating the age- and size-dependency of the timing and duration of spawning (Kjesbu et al. 1996) and egg and larval quality (Solemdal et al. 1993; Marteinsdottir and Steinarsson 1998). These maternal factors can affect not only the quantity of offspring produced but also their survival (Solemdal et al. 1995; Chambers and Leggett 1996; Trippel et al. 1997; Trippel 1998; Nissling et al. 1998).

Indices of the growth rate or physiological condition of spawners could potentially be used as proxies for the reproductive potential of individual spawners and possibly the stock. At the individual level, condition has been shown to influence the potential fecundity of females for a variety of species (Hislop et al. 1978; DeMartini 1991; Koslow et al. 1995; Kjesbu et al. 1998). Condition affects the realized fecundity of spawning females through atresia (Ma et al. 1998) and effects on egg and larval quality (Solemdal et al. 1993; Chambers and Waiwood 1996; Chambers and Leggett 1996; Marteinsdottir and Steinarsson 1998). Condition also affects the annual cycle of gonadal maturation. For example, a laboratory study on captive cod has shown that individuals in poor condition will skip spawning (Burton et al. 1997). At the stock level, anomalously low percentages of mature females in size classes corresponding to repeat spawners were observed in poor condition years suggesting that cod skip spawning seasons (Marshall et al. 1998). Variation in growth rates will affect the rate at which immature fish recruit to the spawning stock. This could be critical to the reproductive potential of the stock, particularly when age diversity is reduced.

In this paper, we examine the relationship between growth–condition of spawners and recruitment for haddock (*Melanogrammus aeglefinus*) on the southwestern Scotian Shelf and Bay of Fundy (NAFO Division 4X). Over the past 30 years, recruitment to age-1 has varied by more than one order of magnitude (Fig. 1A) while spawner biomass has varied by a factor of approximately 4 (Fig. 1B). The recruitment dynamics of this stock remain unexplained despite broad-scale ichthyoplankton surveys conducted in the late 1970s to early 1980s (the Scotian Shelf Ichthyoplankton Program, O'Boyle et al. 1984), process-oriented studies in the mid-1980s (the Fisheries Ecology Program, Smith et al. 1989), population dynamic analysis of the spawner–recruit relationship (O'Boyle et al. 1989), and correlation analysis of the relationship between environmental factors and recruitment (Myers and Drinkwater 1988). The objectives of this study were to (*i*) describe the magnitude of interannual variation in the growth and condition of spawners, (*ii*) examine the relationship between growth and condition of spawners (independent variables) and recruitment (dependent variable), and (*iii*) contrast these relationships with the conventional relationship between VPA-based spawner biomass and recruitment. In essence, this comparison is equivalent to assessing the effects of the quality of individual spawners on recruitment relative to the effects of the quantity of spawners.

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Fig. 1. (A) Time series (1964–1995) of recruitment to age-1 for haddock. (B) Time series (1964–1995) of spawner biomass. Values for 1970 to 1995 were obtained from Hurley et al. (1997), whereas values for 1964 to 1969 were from a specialized run of the VPA described in the text.

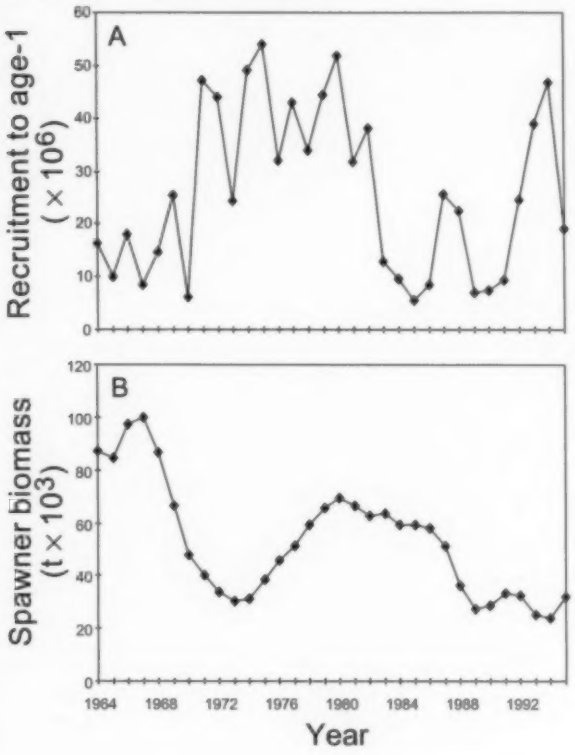
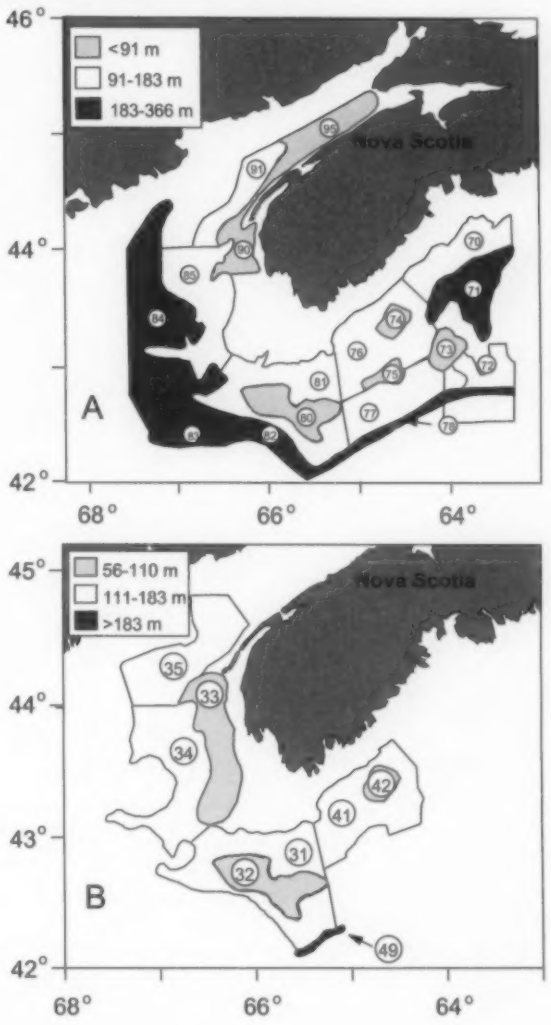


Fig. 2. (A) Strata from Canadian bottom trawl surveys of NAFO Division 4X included in the analysis. (B) Strata from US bottom trawl surveys included in the analysis.



Methods

Data Sources

Indices describing the growth–condition of spawners were developed using data from bottom trawl surveys of the southwestern Scotian Shelf conducted in the spring (1970–1985, with no survey conducted in 1973), summer (1970–1995), and fall (1963–1986). The spring and summer surveys were conducted by the Canadian Department of Fisheries and Oceans (Halliday and Koeller 1981) and the fall survey was conducted by the U.S. National Marine Fisheries Service (Azarovitz 1981). Table 1 indicates the sampling dates for the different survey series. Spring surveys were conducted in February–April, just prior to or at the peak spawning period for haddock in April–May (Page and Frank 1989). Summer and fall surveys were conducted between spawning seasons (Waiwood and Buzeta 1989). For this analysis it was assumed that growth–condition in the summer and fall surveys describe reproductive potential in the subsequent spawning season rather than the preceding one. Thus, the growth–condition of spawners in spawning year $t+1$ was assumed to be sampled by the summer survey in year t, the fall survey in year t, and the spring survey in year $t+1$.

Spring surveys conducted prior to 1979 were based on a fixed station design. With one exception (stratum 91 in 1976), strata located in the Bay of Fundy were not sampled by spring surveys prior to 1979. Canadian (CDN) summer surveys and spring surveys from 1979 to 1985 and the United States (US) surveys use a stratified random design with depth as the major stratifying variable (Fig. 2). Strata boundaries for the CDN surveys were defined using three depth intervals (<100, 100–200, >200 m) that differed slightly from those used in the US surveys (56–110, 111–183, >183 m). The spatial coverage of the CDN surveys (total area 56 734 km^2, 18 strata) better represents the stock range. Strata from the western half of the Bay of Fundy were not included in the analysis because haddock there are considered to belong to the Gulf of Maine stock (Halliday 1974). With the exception of one shallow inshore stratum (stratum 33), the spatial coverage of the US survey (maximum area 29 345 km^2, 8 strata) overlaps with the area sampled by the CDN surveys (Fig. 3). Since 1987, coverage by the US surveys has been reduced to three strata located in the Bay of Fundy (strata 33, 34, and 35). Consequently, these years were not used in the analysis.

Although they are managed as a single stock, haddock on the southwestern Scotian Shelf (SWSS) grow more slowly than haddock in the Bay of Fundy (BofF). Assuming that the commercial

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Fig. 3. Time series (1970–1985, 1973 missing) of mean length at age-4 (solid diamonds) and predicted weight at 50 cm (open squares) for spring surveys.

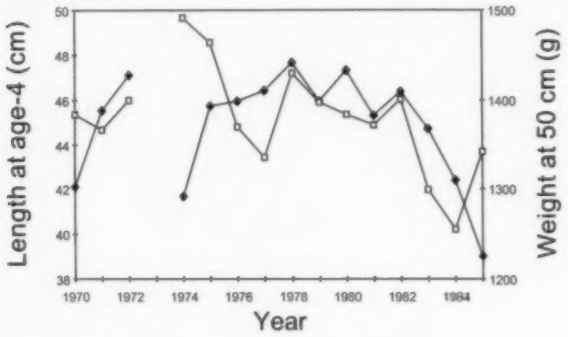
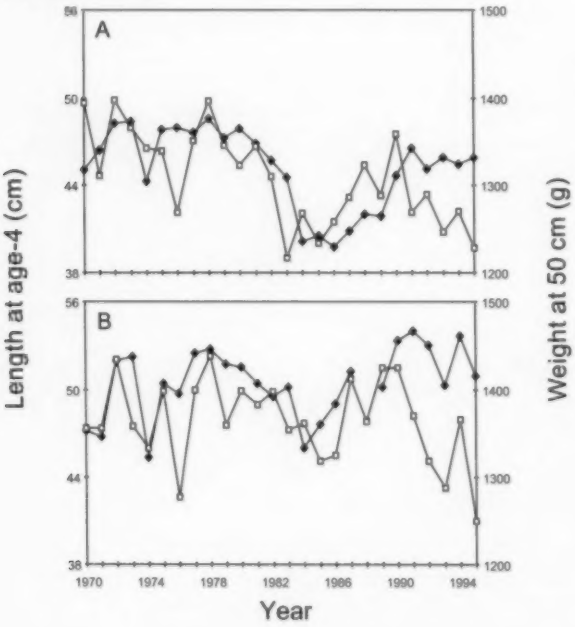
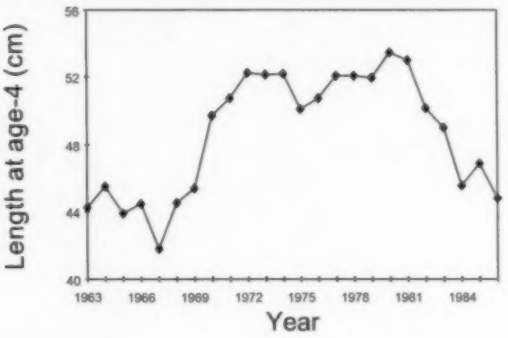


Fig. 4. Time series (1970–1995) of catch-weighted mean length at age-4 (solid diamonds) and predicted weight at 50 cm (open squares) for summer surveys. (A) Southwestern Scotian Shelf; (B) Bay of Fundy.



catch approximates the relative abundance of adult haddock in the two regions, on average 77% of the haddock stock can be found on the SWSS (table 5 in Hurley et al. 1996). Therefore, trends in growth–condition of haddock at the stock level will be dominated by trends observed on the SWSS. The spring, summer, and fall surveys differ with respect to their coverage of the SWSS and BofF regions. Growth–condition indices for the spring survey were calculated for haddock on the SWSS only because the BofF was not included in spring surveys conducted prior to 1979. Growth–condition indices for the summer surveys were calculated for the SWSS (strata 70–81) and the BofF (strata 85, 90, 91, and 95) separately. Strata 82–84 were not included in either grouping because haddock are extremely uncommon in these deep strata. Data for the fall surveys were not subdivided because of the restricted spatial coverage (Fig. 2) and correspondingly fewer observations.

Fig. 5. Time series (1963–1986) of mean length at age-4 for fall surveys.



Consequently, the fall surveys describe the growth of haddock in the SWSS and the BofF combined.

For all surveys, the fork length of individual haddock was recorded to the nearest centimetre. For the CDN surveys, weight was recorded and sagittal otoliths were removed from a length-stratified subsample of the total catch. Prior to 1985, otoliths collected during the CDN surveys were broken and burned for age determinations. Since 1985, age determinations have been made using thin sections along the dorsoventral axis (Strong et al. 1985). In 1993 it was noted that the age estimates for this stock had become systematically biased towards lower values for older haddock (Campana 1995). Consequently, otoliths collected for summer surveys conducted between 1987 and 1995 have been re-aged according to new criteria consistent with criteria used in other haddock-aging laboratories (Hurley et al. 1996). Otoliths for the spring survey have not been re-aged; however, the bias for the time period of the spring surveys (1970–1985) is thought to be minimal (Hurley et al. 1996). For the US surveys, scales were used for young fish and otoliths were used for older fish because of the difficulty in distinguishing the outer annuli on scales (Pentilla and Dery 1988).

Growth and condition indices

The indices used to represent growth and condition of spawners were mean length at age 4 ($\bar{l}_4$) and the predicted weight at a standard length of 50 cm ($\hat{w}_{50}$), respectively. Maturity ogives, constructed by pooling all data for the spring surveys, indicated that the lengths at 50% maturity for haddock in the SWSS and BofF were approximately 37 and 43 cm for males and females, respectively (Waiwood and Buzeta 1989). Values of $\bar{l}_4$ ranged between 38 and 48 cm (spring survey), 38 and 50 cm (summer survey), and 40 and 54 cm (fall survey). Thus, the majority of haddock that are either age-4 or 50 cm in length are mature. Choosing different standard ages or lengths had no effect on any of the general trends observed.

Values of $\bar{l}_4$ were estimated using the length observations for age-4 haddock, including both males and females. Values of $\bar{l}_4$ estimated for the spring and fall surveys were the arithmetic mean of all lengths, uncorrected for the length frequency distribution of the catch. Values of $\bar{l}_4$ for the summer surveys were estimated by correcting for the length distribution of the catch on a stratum-by-stratum basis. The catch-weighted values of $\bar{l}_4$ for the summer survey were significantly different from arithmetic means estimated for the same surveys for both the SWSS (paired t-test, $p = 0.01$, $n = 22$) and the BofF (paired t-test, $p < 0.01$, $n = 22$). The r^2 values for correlations between the catch-weighted and unweighted values of $\bar{l}_4$ were 0.91 and 0.58 for the SWSS and BofF, respectively. Using unweighted values will therefore have a greater effect on analysis of data from the BofF relative to the SWSS.

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Table 2. Summary statistics for regressions describing the relationship between recruitment to age-1 (thousands) and body size characteristics of adult haddock for spring, summer, and fall surveys of the southwestern Scotian Shelf (SWSS) and Bay of Fundy (BofF).

Survey/source	Indep. var.	Region	Year-classes	r^2	p^*
Spring	$\bar{l}_4$	SWSS	1970–1985	0.41	0.01
Spring	$\bar{l}_4$	SWSS	1970–1985, exc. 1974	0.66	<0.01
Summer	$\bar{l}_4$	SWSS	1971–1995	0.35	<0.01
Fall	$\bar{l}_4$	SWSS/BofF	1964–1987	0.51	<0.01
Spring	$\hat{w}_{50}$	SWSS	1970–1985	0.37	0.01
Summer	$\hat{w}_{50}$	SWSS	1971–1995	0.18	0.04
Summer	$\hat{w}_{50}$	SWSS	1971–1991	0.28	0.02
Summer	$\bar{l}_4$	BofF	1971–1995	<0.01	0.85
Summer	$\hat{w}_{50}$	BofF	1971–1995	0.09	0.15
Summer	$\hat{w}_{50}$	BofF	1971–1991	0.05	0.35
VPA	ssb	SWSS/BofF	1964–1995	0.07	0.15

Note: The independent variables are mean length at age-4 ($\bar{l}_4$) and predicted weight at a standard length of 50 cm ($\hat{w}_{50}$). Values of p^* have been corrected for temporal autocorrelation as described in the text. Statistics are also given for the relationship between recruitment and the VPA estimate of spawner biomass (ssb).

To estimate $\hat{w}_{50}$, length (l) and weight (w) observations were used to fit the equation

$$(1) \qquad \log_{10}(w) = \log_{10}(\alpha) + \beta \log_{10}(l)$$

for each survey. For this index, only observations for female haddock were used. For spring surveys, only ripening and spawning females (maturity stages 3–5; Waiwood and Buzeta 1989) were included in the weight–length regressions for the spring surveys. For the summer surveys, all females age-3 and older were considered mature. Where age estimates were missing, observations for female haddock 37 cm in length or larger were included in the data set. No temporal trend in the length range of observations included in the regression data sets was noted although the number of observations varied according to total abundance. Trends in $\hat{w}_{50}$ could not be examined for the fall surveys because the US surveys did not systematically record individual weight.

Recruitment and spawner biomass

The abundance of age-1 haddock from 1970 to 1995 (Hurley et al. 1997) was used as an index of recruitment for the 1969–1994 year-classes. The abundance of age-1 haddock from 1965–1969 was obtained from a specialized VPA run described below. For the spring surveys, growth–condition in survey year t was correlated with the recruitment index for spawning year t. Correlations for the summer and fall surveys were lagged by 1 year such that growth–condition in survey year t was correlated with the recruitment index for spawning year $t + 1$.

A specialized run of the age-based VPA was used to generate estimates of spawner biomass for the time period 1962–1969 (P.C.F. Hurley, Marine Fish Division, Bedford Institute of Oceanography, P.O. Box 1006, Dartmouth, N.S., Canada). Because the CDN research survey series did not begin until 1970, commercial weight at age was used to calculate spawner biomass. As in Hurley et al. (1997), a constant maturity ogive (O'Boyle et al. 1989) was used to estimate spawner biomass.

Autocorrelation correction

In estimating the statistical significance of the correlations between recruitment and growth–condition the number of observations in the time series was corrected for autocorrelation by

$$(2) \qquad n^* = \frac{n}{1 + 2r_1 r_1' + 2r_2 r_2'}$$

where n is the number of observations in each of the two time series, r_1 and r_1' are the lag-one autocorrelations of the two series, and r_2 and r_2' are the lag-two autocorrelations of the two series (Quenouille 1952). Higher-order autocorrelations were not included in the correction. Corrected p values reported here (p^*) have been estimated using the corrected degrees of freedom.

Results

Temporal trends in growth and condition

The spring survey for the SWSS shows that both $\bar{l}_4$ and $\hat{w}_{50}$ were relatively stable until 1982 when both indices began to decrease (Fig. 3). The differences between maximum and minimum values in the time series expressed as a percentage of the minimum (Δ%) were 22 and 19% for $\bar{l}_4$ and $\hat{w}_{50}$, respectively. The value of $\bar{l}_4$ in 1974 was unusually low relative to adjacent years and at odds with the trend observed in $\hat{w}_{50}$.

The summer survey for the SWSS (Fig. 4A) confirms that $\bar{l}_4$ and $\hat{w}_{50}$ were relatively high and stable from 1972 to 1980, then decreased during 1981–1983, and remained low until 1986 when the values began to increase. As in the spring survey, $\bar{l}_4$ in 1974 was low relative to adjacent years. Over the entire time period, the values of Δ% were 22 and 15% for $\bar{l}_4$ and $\hat{w}_{50}$, respectively. The temporal trends observed in $\bar{l}_4$ and $\hat{w}_{50}$ are reasonably synchronous until the most recent years (1991–1995) when the trends diverged. During this time period, $\bar{l}_4$ increased to values that are near those observed between 1972 and 1980, while $\hat{w}_{50}$ decreased to values that are nearly 200 g lower than those observed in 1972–1980.

Growth rates differ between the BofF and the SWSS both with respect to magnitude and temporal trends (Fig. 4B). Haddock in the BofF are longer at age and heavier at length compared with haddock on the SWSS. Over the entire time period, values of $\bar{l}_4$ in the BofF show an increasing trend and in recent years (1991–1995) have been at or near historical highs. The $\bar{l}_4$ value for 1974 was again low relative to adjacent values. Unlike the SWSS, the mid-1980s were not characterized by historical lows in both $\bar{l}_4$ and $\hat{w}_{50}$. Values of Δ%

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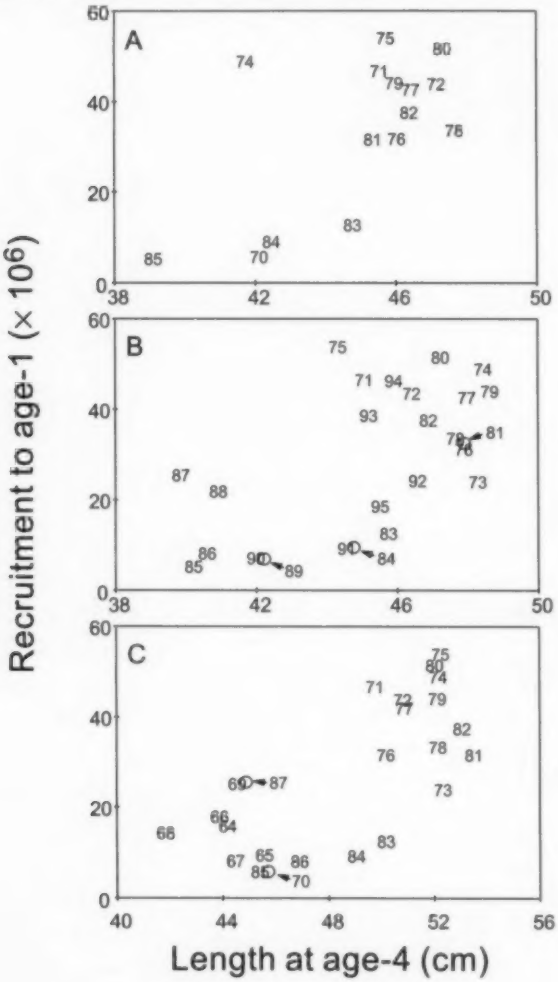
Fig. 6. Relationship between recruitment to age-1 and mean length at age-4 of haddock on the southwestern Scotian Shelf. Observations are identified by the spawning year. (A) Spring survey; (B) summer survey; (C) fall survey.



were 19 and 15% for $\bar{l}_4$ and $\hat{w}_{50}$, respectively. After a period of relatively synchronous variation, a divergence between $\bar{l}_4$ and $\hat{w}_{50}$ has occurred in recent years (1991–1995). Values of $\bar{l}_4$ are near historical highs, whereas values of $\hat{w}_{50}$ are at or near historical lows. The decoupling of trends in $\bar{l}_4$ and $\hat{w}_{50}$ for both the SWSS and BofF cannot be attributed to a change in timing of the summer survey because there was no systematic shift towards earlier or later surveys during that time period (Table 1).

The fall survey for southernmost portions of both SWSS and the BofF (SWSS–BofF) shows low values of $\bar{l}_4$ from 1963–1967, suggesting that conditions for growth of haddock were poor during this time period (Fig. 5). Values of $\bar{l}_4$ increased rapidly from 1967 to 1972, were high throughout the 1970s, and then began to decrease in 1981, a temporal trend that is consistent with those observed in the spring and summer surveys. The value of $\Delta\%$ for $\bar{l}_4$ was 28%.

Fig. 7. Relationship between recruitment to age-1 and predicted weight at 50 cm of haddock on the southwestern Scotian Shelf. Observations are identified by the spawning year. (A) Spring survey; (B) summer survey.

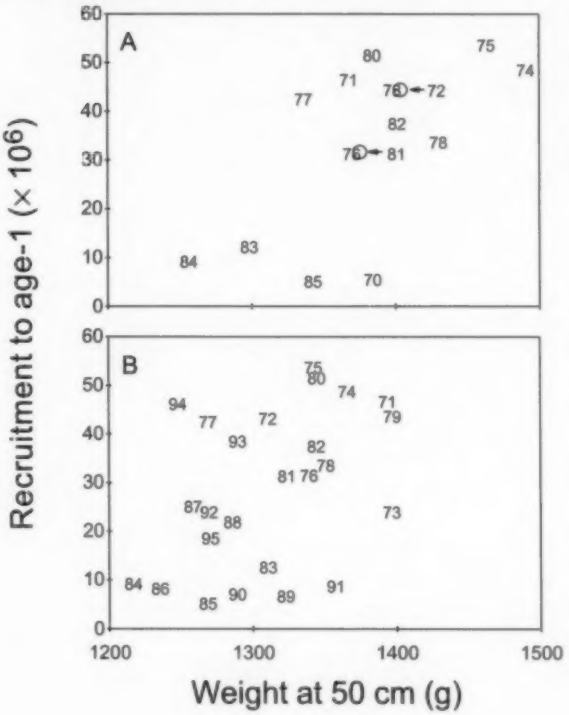
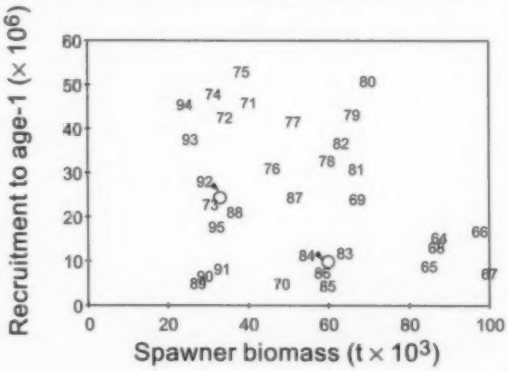


Fig. 8. Relationship between recruitment to age-1 and spawner biomass. Observations are identified by the spawning year.



Relationship between recruitment and body size of spawners

For haddock on the SWSS there were significant ($p^* \leq 0.01$) positive correlations between recruitment and $\bar{l}_4$ for the spring, summer, and fall surveys (Table 2). Time periods associated with poor growth and low values of $\bar{l}_4$ (the 1960s and mid-1980s) had low values of recruitment, whereas recruitment was high in periods when haddock were larger (the 1970s and early 1980s) (Fig. 6). The 1974 year-class

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Table 3. Significance levels associated with the partial (Type II) sums of squares for a multivariate model having a body size variable (either $\bar{l}_4$ or $\hat{w}_{50}$) and a stock abundance variable (either spawner biomass (ssb) or total abundance of haddock age-4 and older (total 4+)) as the independent variables.

Survey	Time period	Body size variable	Stock abundance variable	Partial SS
Spring	1970–1985	$\bar{l}_4$	ssb	0.06 (<0.01)
			total 4+	0.02 (<0.01)
Summer	1971–1995	$\bar{l}_4$	ssb	0.74 (<0.01)
			total 4+	0.54 (<0.01)
Fall	1964–1987	$\bar{l}_4$	ssb	0.55 (<0.01)
			total 4+	0.54 (<0.01)
Spring	1970–1985	$\hat{w}_{50}$	ssb	0.92 (0.03)
			total 4+	0.41 (0.07)
Summer	1971–1995	$\hat{w}_{50}$	ssb	0.99 (0.04)
			total 4+	0.73 (0.04)

Note: Recruitment to age-1 is the dependent variable. The partial SS was calculated for each stock abundance variable assuming that the body size variable was already in the model. The partial SS for the body size variable is given in brackets (i.e., the significance of the body size variable assuming the stock abundance variable was already in the model).

was an outlier for the spring survey (Fig. 6A) but not the summer (Fig. 6B) or fall surveys (Fig. 6C). Excluding this observation from the correlation increased the r^2 value for the spring survey from 0.41 to 0.66 (Table 2).

Recruitment was also significantly, positively correlated (Table 2) with $\hat{w}_{50}$ for haddock on the SWSS for both the spring (Fig. 7A) and summer surveys (Fig. 7B). Compared with the relationship between recruitment and $\bar{l}_4$ (Fig. 6), the relationship between recruitment and $\hat{w}_{50}$ was weaker (Table 2). The stronger relationship between recruitment and $\hat{w}_{50}$ for the spring survey (Fig. 7A) compared with the summer survey (Fig. 7B) suggests that the condition of spawners at or near the time of spawning would be a better proxy for reproductive potential and therefore a stronger correlate of recruitment. Given that there has been a divergence between $\bar{l}_4$ and $\hat{w}_{50}$ in recent years (Fig. 4), observations for the 1991–1995 year-classes were deleted from the correlation between recruitment and $\hat{w}_{50}$ for the summer survey. This had the effect of increasing the r^2 value from 0.18 to 0.28 (Table 2), which is still lower than the r^2 values for the correlation between recruitment and $\bar{l}_4$ for the summer survey.

There were no significant correlations between recruitment and either $\bar{l}_4$ or $\hat{w}_{50}$ for haddock in the BofF (Table 2). Deleting the observations for 1991–1995 had a negligible effect on the level of significance for the relationship between recruitment and $\hat{w}_{50}$ (Table 2).

Relationship between recruitment and spawner biomass

There was no discernable relationship between recruitment and spawner biomass (Fig. 8; Table 2), which is consistent with all previous studies of the stock–recruit relationship for 4X haddock. This result contrasts with the significant, positive correlations observed between recruitment and body size characteristics of spawners (Figs. 6 and 7). For example, the 1964–1969 year-classes were weak despite high spawner biomass (Fig. 8). However, this time period was associated with poor growth and smaller body size of spawners (Fig. 5). This appears to have had a greater influence on recruitment (Fig. 6C). Similarly, the 1970s are associated with low to intermediate spawner biomass (Fig. 8); however, haddock were larger and recruitment was high (Figs. 6 and 7).

The effect of variation in the quantity of spawners on the recruitment–body size relationships in Figs. 6 and 7 was investigated using multivariate models that included a term for the body size of individual spawners ($\bar{l}_4$ or $\hat{w}_{50}$) and stock abundance (VPA-based estimates of spawner biomass or total abundance of haddock age-4 and older). With the sole exception of the model for spring survey having $\bar{l}_4$ and the total abundance of haddock age-4 and older (total 4+) as the independent variables, the addition of a stock abundance variable to a model already containing the body size variable did not significantly decrease the model sum of squares (Table 3). However, the addition of the body size variable to a model already containing the stock abundance variable always resulted in a significant decrease in the model sum of squares. Thus, the effect of the quantity of spawners on recruitment is less significant than the effect of the body size characteristics (quality) of spawners.

Discussion

A significant, positive correlation between recruitment and the body size characteristics of mature haddock on the SWSS was observed for spring, summer, and fall surveys, which in combination, cover a period of approximately 3 decades (1964–1995). The recruitment–body size correlation is analagous to the positive correlation between recruitment and age diversity noted for Icelandic cod (Marteinsdottir and Thorarinsson 1998) in that it implicates interannual variation in the reproductive potential in the recruitment dynamics of gadoid stocks. When contrasted with the indeterminate relationship between recruitment and VPA-based spawner biomass for haddock (Fig. 8), it suggests that spawner biomass is an inaccurate and (or) biased measure of the reproductive and hence recruitment potential. This conclusion is consistent with the recent studies for Icelandic cod (Marteinsdottir and Thorarinsson 1998) and NEA cod (Marshall et al. 1998).

In the absence of estimates of total egg production or abundance, proxy variables describing the growth–condition of spawners may provide insight into the recruitment dynamics of a stock. At the individual level there is ample evidence that the fecundity of long-lived gadoids such as cod and haddock varies according to growth and condition. For example, the fecundity of captive haddock has been shown to be positively correlated with condition and food ration (Hislop et al. 1978). Interannual variation in the fecundity–length relationship for wild NEA cod has been attributed to variation in condition (Kjesbu et al. 1998). There is a higher incidence of atresia in cod that are in poor condition because of food limitation (Kjesbu et al. 1991). Egg quality also varies according to body size characteristics of spawners. Egg size of haddock is positively correlated with length (Hislop 1988). Similarily, the egg diameter of cod was correlated with length (Solemdal et al. 1993) and (or) condition (Chambers and Waiwood 1996; Marteinsdottir and Steinarsson 1998). Both the body size of larval fish and their abil-

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ity to withstand starvation may also be influenced by maternal condition (Chambers and Leggett 1996).

At the stock level, variation in the growth–condition of individual fish could influence the reproductive potential of gadoid stocks in several different ways. Growth–condition determines the rate at which immature fish become recruit (first-time) spawners. This will obviously affect the reproductive potential of the stock, particularly as smaller fish generally have the advantage of higher numerical abundance. Faster growth and maturation could increase the probability that fish survive long enough to contribute to total egg production both as recruit and as repeat spawners. A positive, non-linear relationship between the proportion of eggs produced by repeat spawning NEA cod and recruitment (Marshall et al. 1998) suggests that this variation in this demographic feature of gadoid stocks might contribute to recruitment variation. Similarly, Hislop (1988) recommended downweighting the egg contribution of recruit-spawning North Sea haddock because they produce significantly smaller eggs. Variation in growth–condition may affect the seasonal maturation dynamics of repeat spawners disproportionately because relative to recruit spawners repeat spawners experience more severe depletion of body reserves and are therefore more sensitive to variations in feeding regimes (Kjesbu and Holm 1994). Skipped spawning seasons have been suggested for NEA cod in poor condition (Marshall et al. 1998). Likewise, mature female walleye (*Stizostedion vitreum*) in poor condition are unlikely to ripen and spawn (Henderson et al. 1996). Spawner biomass values estimated using knife-edge or sigmoidal maturity ogives do not allow for the possibility of skipped spawning seasons (Trippel and Harvey 1991). This will overestimate the effective spawner biomass when a substantial portion of the repeat spawners are non-reproductive (Burton et al. 1997).

The quantity of spawners obviously determines reproductive potential when stock abundance is extremely low (e.g., stock collapse). In more usual circumstances (e.g., the range in spawner biomass depicted in Fig. 1B), the effect of quantity may not be straightforward. Future recruitment research must clearly differentiate the effects of quality of individual spawners on growth, condition, maturation rates, and fecundity from the effects of quantity of spawners when assessing the reproductive potential of a stock (MacKenzie et al. 1998). This study has shown how routinely collected body size information can be used as proximate measures of reproductive potential. Other proxy variables are easily envisaged, e.g., liver condition index, gonadosomatic index. Examining the relationships between recruitment and proxy variables is a cost-effective interim measure for examining stock effects on recruitment variation. Estimates of total egg production or abundance, which account for both the quantity and quality of spawners, constitute the ultimate test.

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Implications of density-dependent juvenile growth for compensatory recruitment regulation of haddock

C. Tara Marshall and Kenneth T. Frank

Abstract: Data from bottom trawl surveys conducted by Canada and the United States were used to describe temporal trends in the length of haddock ages 1–4 on the southwestern Scotian Shelf (SWSS) and Bay of Fundy. From 1970 to 1995, the length of juvenile (age-1) haddock on the SWSS was negatively correlated with the abundance of adults (age-4+). Within year-classes temporal trends in juvenile length persisted through to the adult stage such that year-classes that were small(large) at age-1 were small(large) at age-4. These two results were combined with the positive correlation observed between recruitment and the body size characteristics of haddock on the SWSS in a conceptual model of compensatory recruitment regulation. In the model high adult abundance decreases growth of juveniles leading to smaller-sized adults and subsequently lower recruitment. Conversely, low adult abundance results in increased growth of juveniles leading to larger adults and higher recruitment. Density-dependent growth of juveniles, combined with the positive correlation between recruitment and adult body size, constitutes a compensatory mechanism for adjusting future haddock recruitment according to present adult abundance.

Résumé : On a utilisé les données de campagnes d'échantillonnage au chalut de fond réalisées par le Canada et les États-Unis pour décrire les tendances temporelles des longueurs de l'aiglefin de 1 à 4 ans dans le sud-ouest de la plate-forme néo-écossaise et la baie de Fundy. De 1970 à 1995, la longueur de l'aiglefin juvénile (âge 1) dans le sud-ouest de la plate-forme néo-écossaise était corrélée négativement avec l'abondance des adultes (âges 4+). Les tendances temporelles de la longueur des juvéniles à l'intérieur des classes d'âge ont persisté jusqu'à l'âge adulte en ceci que les poissons qui étaient petits (ou gros) à l'âge 1 étaient petits (ou gros) à l'âge 4. Ces deux résultats ont été combinés avec la corrélation positive observée entre le recrutement et les caractéristiques de taille de l'aiglefin dans le sud-ouest de la plate-forme néo-écossaise dans un modèle conceptuel de régulation compensatoire du recrutement. Selon ce modèle, une forte abondance des adultes entraîne une baisse de la croissance des juvéniles, qui deviendront des adultes de plus petite taille, d'où un recrutement subséquent réduit. Inversement, une faible abondance d'adultes augmente la croissance des juvéniles, qui deviendront des adultes de plus grande taille, d'où un recrutement subséquent accru. Le fait que le taux de croissance des juvéniles dépende de la densité, combiné avec la corrélation positive entre le recrutement et la taille des adultes, constitue un mécanisme compensatoire qui ajuste le recrutement futur des aiglefins à l'abondance présente des adultes.

[Traduit par la Rédaction]

Introduction

Investigations into the density-dependent responses of haddock (*Melanogrammus aeglefinus*) stocks have a long history. Herrington (1944) proposed that when adult haddock on Georges Bank were abundant they depleted available food resources (the macrobenthos) and then moved on to other feeding grounds, leaving the more sedentary juveniles to experience food limitations, which increased their mortality. Herrington suggested that the competitive interaction between juvenile and adult haddock resulted in recruitment being highest for intermediate levels of stock abundance (fig. 5 in Herrington 1944). His analysis was one of several examples used by Ricker (1954) in formulating the dome-shaped relationship between recruitment and spawner abundance. Increased competition between juveniles and adults for a shared food resource could also decrease the growth of juveniles. While density-dependent growth has been observed in a majority of studies on haddock growth (Table 1), few of these studies specifically examined the relationship between juvenile growth rate and adult abundance.

The growing appreciation of maternal effects on the recruitment dynamics of gadoid stocks (Marteinsdottir and Thorarinsson 1998; Marshall et al. 1998) introduces new possibilities for linking density-dependent responses to recruitment. The companion paper (Marshall and Frank 1999) found that recruitment to age-1 is positively correlated with length and (or) condition of spawning haddock on the southwestern Scotian Shelf portion of NAFO Division 4X. This correlation focuses attention on identifying the factors that

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Table 1. Summary of studies investigating the relationship between stock abundance and growth of haddock.

Year	Time period	Correlation	Reference
North Sea	1923–1931	None	Bowman 1932
North Sea	1919–1934	Negative	Raitt 1936
Skagerak	1929,1938	Negative	Andersson 1938
North Sea	1919–1938	Negative	Raitt 1939
Georges Bank	1912–1946	Negative	Herrington 1948
Barents Sea	1945–1959	Negative	Sonina 1965
Grand Bank	1940–1975	Negative	Templeman et al. 1978
North Sea	1923–1972	Negative	Jones 1979
St. Pierre Bank	1948–1975	Negative	Templeman and Bishop 1979
Browns Bank	1970–1979	Negative	Beacham 1982
Georges Bank	1930–1980	Negative	Clark et al. 1982
North Sea	1959–1971	Negative	Jones 1983
North Sea	1960–1980	Negative	Cook and Armstrong 1984
North Sea	1977–1985	None	Bromley 1989
Georges Bank	1963–1980	Negative	Ross and Nelson 1992

generate differences in body size characteristics of adults among year-classes. The degree to which size differences observed at the juvenile stage persist through to the adult stage is of interest for the following reason: a negative correlation between stock abundance and juvenile growth that persists through to the adult stage combined with a positive correlation between adult body size and recruitment constitutes a compensatory mechanism for regulating recruitment.

Over the past 3 decades, the abundance of adult haddock in NAFO Division 4X (see fig. 2 in Marshall and Frank (1999) for map) shows two distinct peaks (Fig. 1). The first peak was fueled by the exceptionally strong 1962 and 1963 year-classes, whereas the second peak from 1979 to 1986 reflects a sustained period of good recruitment in the 1970s and early 1980s (fig. 1B in Marshall and Frank (1999) gives the recruitment time series). The effect of adult abundance on juvenile growth specifically is unknown. Data from research vessel surveys conducted by Canada and the United States were used to address the following questions: (*i*) what is the pattern of temporal variation in juvenile body size, (*ii*) how has the growth of juveniles responded to changes in adult abundance, and (*iii*) do differences among year-classes in juvenile body size persist through to the adult stage such that small juveniles become small adults? The effect of interannual variation in bottom water temperature on juvenile growth was also evaluated. The results were combined with the relationship between recruitment and the body size characteristics of adults (Marshall and Frank 1999) in a conceptual model describing a possible form of compensatory recruitment regulation in Scotian Shelf haddock.

Methods

The data sources used to describe temporal variation in body size characteristics of juvenile haddock in Division 4X were the summer (1970–1995) and fall (1963–1986) surveys conducted by Canada (CDN) and the United States (US), respectively. Temporal and spatial coverage of these surveys are described in Marshall and Frank (1999). Because haddock in the Bay of Fundy are larger than haddock on the southwestern Scotian Shelf (fig. 4 in Marshall and Frank (1999)), the survey database was partitioned into two distinct geographic regions: the southwestern Scotian Shelf (SWSS) and Bay of Fundy (BofF). For the CDN surveys, data from strata 70–81 were used to represent the SWSS and data from strata 85, 90, 91, and 95 were used to represent the BofF (fig. 2A in Marshall and Frank (1999)). For the US surveys, data from strata 31, 32, 41, 42, and 49 were used to represent the SWSS and data from strata 33, 34, and 35 were used to represent the BofF (fig. 2B in Marshall and Frank (1999)).

Mean length at age was used as an index of growth for haddock age-1 to age-4. For the CDN surveys, the catch-weighted mean length at age was estimated by weighting the length observations for the length frequency distribution of the trawl catches. Mean length at age for the US surveys was calculated as the arithmetic average of all of the length observations for a given age class in strata in that region (either SWSS or BofF). Correlations between the CDN and US values for the overlapping time period (1970–1986) were examined to determine if temporal trends in the unweighted US estimates of mean length at age agreed with the catch-weighted CDN estimates. The p values reported were corrected for temporal autocorrelation (p^*) using eq. 2 in Marshall and Frank (1999). There were significant ($p^* \leq 0.05$) positive correlations between CDN and US mean lengths for all four age classes on the SWSS and for haddock age-2 to age-4 in the BofF (Table 2). The correlation between CDN and US mean length at age-1 for the BofF was not significant ($p^* = 0.42$) even when the outlying observation for 1972 was excluded ($p^* = 0.54$). The weaker correlations for age-1 haddock suggest that size-dependent catchability might be introducing error into estimates of mean length for the smallest fish (Engås and Godø 1989).

The correlation between length at age-1 and adult abundance was examined using the total abundance of haddock age-4 and older as an estimate of adult abundance (Fig. 1). From 1979–1985, the ages at 50% maturity ranged from 2.8 to 3.6 years for female haddock in Division 4X and from 2.8 to 3.3 years for males (Trippel et al. 1997*a*). Thus, the total abundance of haddock age-4 and older approximates the abundance of a fraction of the stock which is >50% mature. Abundance at age for 1970–1995 was estimated using Virtual Population Analysis (VPA) (Hurley et al. 1997). Abundance at age for 1963–1969 was generated using a specialized VPA run (P.C.F. Hurley, Marine Fish Division, Bedford Institute of Oceanography, P.O. Box 1006, Dartmouth, N.S., Canada).

The influence of temperature on the growth of juvenile haddock was also assessed. Water temperatures, expressed as anomalies from the long-term average (1961–1990), are available by month for 35 subareas of the Scotian Shelf (Drinkwater and Trites 1987).

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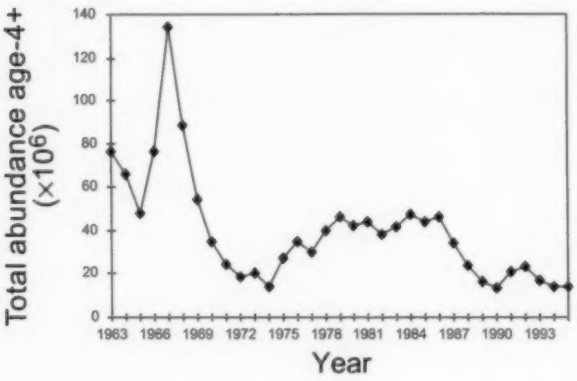
Fig. 1. Temporal trends (1863–1995) in total abundance of haddock age-4 and older. Values for 1970 to 1995 were obtained from Hurley et al. (1997), whereas values for 1963 to 1969 were from a specialized VPA run described in Marshall and Frank (1999).



Data for subarea 22 (corresponding to stratum 80) and subarea 24 (corresponding to stratum 85) were used to represent temperatures on the SWSS and BofF, respectively. Temperature anomalies at depths of 100 and 50 m were used for subareas 22 and 24, respectively. Mean temperature anomalies for the CDN survey were calculated by pooling observations for June and July. Observations for October and November were pooled to estimate the mean temperature anomalies at the time of the US survey. There were several years of missing observations for the June–July and October–November time periods.

In the model of compensatory recruitment regulation, only CDN data for the SWSS were used. This was done because (*i*) the correlation between recruitment and mean length at age-4 was significant for the SWSS but not for the BofF (table 2 in Marshall and Frank (1999)) and (*ii*) haddock on the SWSS constitute approximately 75% of the commercial catch of the 4X haddock stock (table 3 in Hurley et al. 1997) and the recruitment dynamics of this component will have the greatest influence on the stock. Cross correlation analysis of the CDN mean length at age time series for the SWSS was used to determine whether temporal trends in length at age-1 persisted as the year-class aged. If there is a year-class effect on growth then peak correlations would occur at appropriate lags (e.g., the peak correlation between length at age-1 and length at age-4 would occur at a 3-year lag). The correlation between length at age-1 and length at age for the three older age classes was determined for six different lags (–1 to 5 years).

A key element of the conceptual model describing compensatory recruitment regulation is the relationship between recruitment to age-1 and mean length at age-4, which was developed for haddock on the SWSS in the companion paper (see fig. 6B in Marshall and Frank (1999)). Given that haddock spawn in the spring, this relationship was developed assuming that mean length at age-4 observed at the time of the CDN summer survey in year t represents the reproductive potential of spawners in year $t + 1$. Therefore, the relationship is between recruitment in year $t + 1$ (i.e., abundance of age-1 haddock in year $t + 2$) and mean length at age-4 in year t.

Results

For the CDN surveys, length at age-1 on the SWSS decreased by approximately 4 cm from the mid-1970s to a minimum in 1981 (Fig. 2A). Length at age-1 then increased such that by the 1990s lengths were comparable with those observed earlier in the time series. The temporal trends observed for haddock age-2 to age-4 on the SWSS from 1970 to 1995 (Figs. 2B–2D) were similar to those for age-1 haddock with minimum lengths occuring in the mid-1980s. The minimum length at age-4 was observed in 1984 (i.e., 3 years after the minimum in length at age-1). Lengths for all four age classes were almost always higher in the BofF (Figs. 2A–2D) compared with the SWSS. Unlike the SWSS, length at age was not at a minimum in the BofF in the 1980s. Length at age-1 for the BofF showed no distinct temporal trend although the observation for 1972 was anomalously low relative to all other values. A slight decrease in length at age was observed during the late 1970s for older haddock in the BofF.

Table 2. The coefficient of determination and corrected significance levels (p^* in brackets) for correlations between the US mean length at age and CDN length at age for 1970–1986 for the southwestern Scotian Shelf (SWSS) and Bay of Fundy (BofF).

Age	SWSS	BofF
1	0.24 (0.05)	0.05 (0.42)
2	0.65 (<0.01)	0.54 (<0.01)
3	0.83 (<0.01)	0.25 (0.05)
4	0.79 (<0.01)	0.56 (<0.01)

For the US surveys, haddock on the SWSS exhibited minimum length at age values in the 1960s for all four age classes (Fig. 3). From 1963 to 1966, length at age-1 on the SWSS decreased by approximately 6 cm (Fig. 3A) and was at a minimum in 1966 and 1967 when adult abundance was at or near maximum (Fig. 1). A slight decreasing trend in length at age-1 began on the SWSS in the late 1970s and continued through the early 1980s. The lengths for haddock age-2 to age-4 on the SWSS were also low in the mid-1960s, increased from 1967 to 1971, and then began to decrease in the late 1970s or early 1980s (Figs. 3B–3D). Length for haddock age-1 to age-4 in the BofF exhibited low values in the mid-1960s followed by a rapid increase (Figs. 3A–3D). Unlike the SWSS there was no evidence of a decrease in length at age beginning in the late 1970s.

On the SWSS, length at age-1 is negatively correlated with adult abundance ($r^2 = 0.30$, $p^* < 0.01$) for the CDN survey such that length at age-1 was low in the late 1970s to mid-1980s when adult abundance was high (Fig. 4A). The correlation between length at age-1 and adult abundance for haddock on the BofF was not significant ($r^2 = 0.03$, $p^* = 0.40$) for the CDN survey (Fig. 4B). For the US survey, the results were reversed: the correlation between mean length at age-1 and adult abundance was not significant for the SWSS ($r^2 = 0.07$, $p^* = 0.23$, Fig. 4C) but was significant for the BofF ($r^2 = 0.26$, $p^* = 0.03$, Fig. 4D).

For the SWSS, mean length at age-1 was uncorrelated with temperature anomalies in both the CDN and US surveys, irrespective of whether temperature was the only variable in a univariate model or the second variable added to a bivariate model that included adult abundance (Table 3). This was also true for the BofF for the time period covered by the CDN survey. For the US survey of the BofF, the temperature anomaly term was significant (Table 3) when it was

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Fig. 2. Temporal trends in catch-weighted mean length at age of haddock for CDN surveys (1970–1995). Open squares are for values for the southwestern Scotian Shelf and closed diamonds are values for the Bay of Fundy. (A) Age-1; (B) age-2; (C) age-3; (D) age-4.

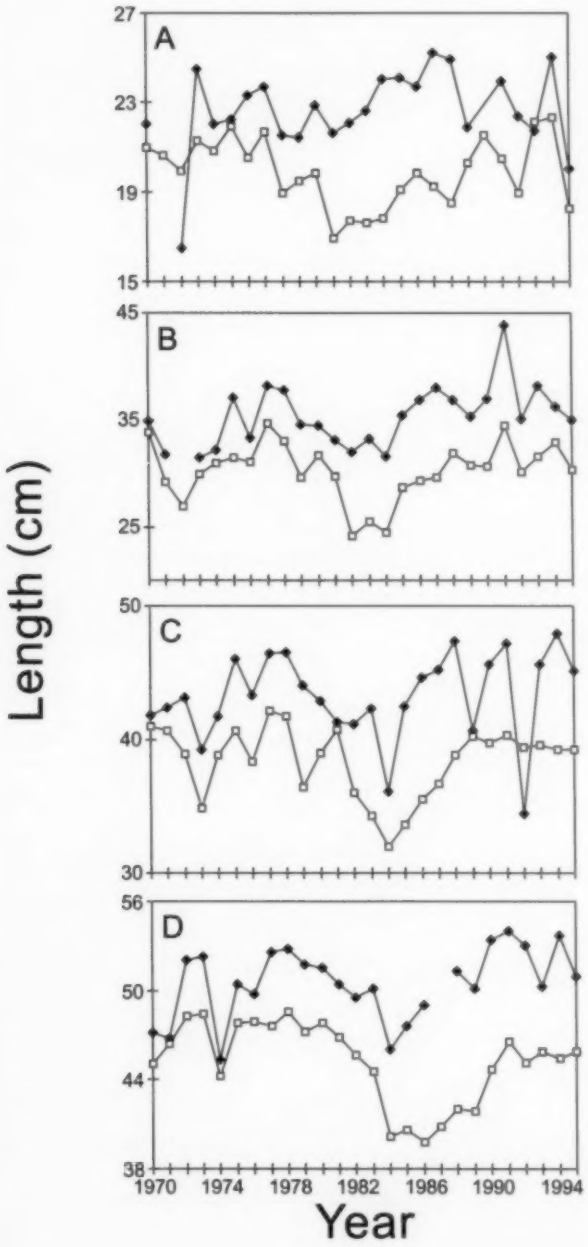
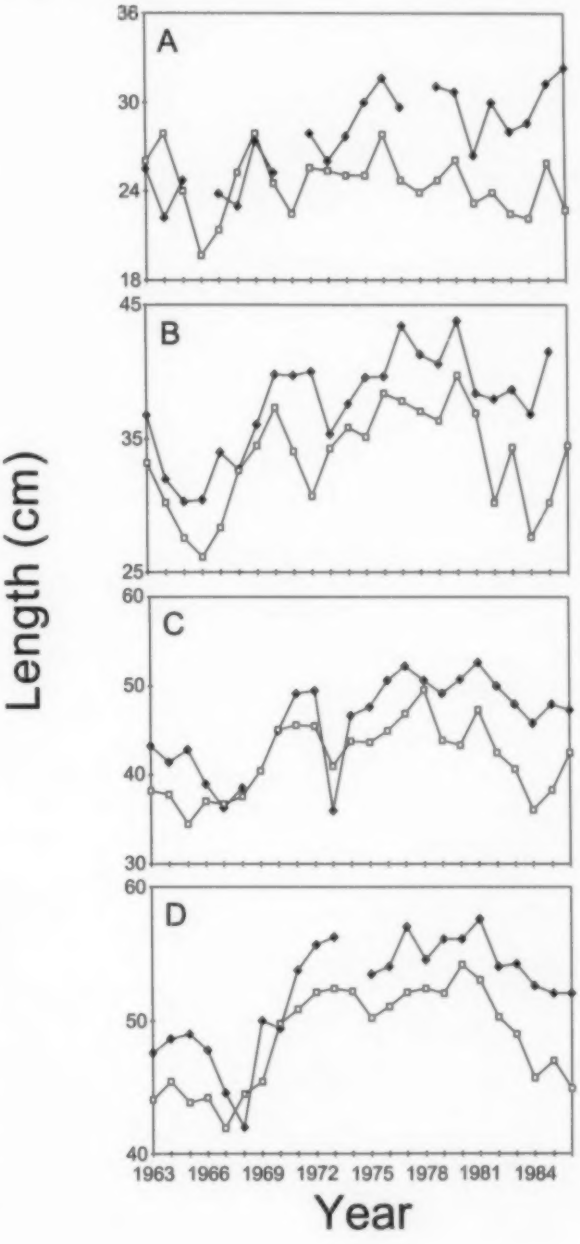


Fig. 3. Temporal trends in mean length at age of haddock for US surveys (1963–1986). Open squares are values for the southwestern Scotian Shelf and closed diamonds are values for the Bay of Fundy. (A) Age-1; (B) age-2; (C) age-3; (D) age-4.



the only variable in a univariate model. It was not significant in a bivariate model that included adult abundance.

The strongest evidence of a negative correlation between juvenile growth and adult abundance is for the SWSS during the time period covered by the CDN survey (1970–1995; Fig. 4A). This time period on the SWSS is also characterised by a positive correlation between recruitment and length at age-4 (fig. 6B in Marshall and Frank (1999)). To link these two relationships together it was necessary to ex-

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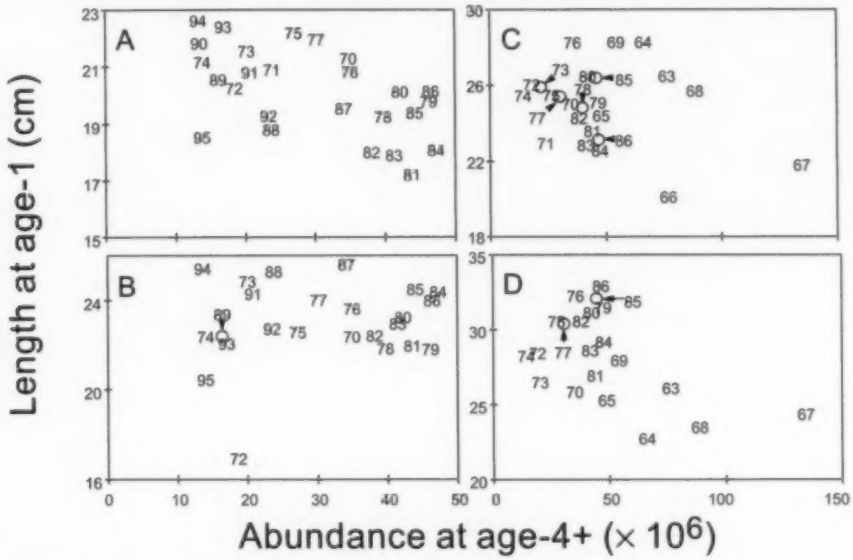
Fig. 4. Relationship between mean length at age-1 and adult abundance. Labels denote the observational year. Note the difference between left- and right-hand panels with respect to the magnitude of the *x* axis. (A) Southwestern Scotian Shelf (CDN survey); (B) Bay of Fundy (CDN survey); (C) southwestern Scotian Shelf (US survey); (D) Bay of Fundy (US survey).



amine whether size differences established at the juvenile stage persist through to the adult stage. For haddock on the SWSS (CDN survey), temporal trends in length at age-1 persisted as the year-class aged (Fig. 5). The peak correlations between length at age-2 and length at age-1 and between length at age-4 and length at age-1 occurred at the expected lags (1 and 3 years, respectively) although the peak lag for the correlation between length at age-1 and length at age-3 occurred 1 year earlier than expected. Thus, from 1970 to 1995, the differences in body size observed at the juvenile stage for SWSS haddock persisted through to the adult stage.

The interrelationships between adult abundance, juvenile and adult body size, and recruitment were combined in a conceptual model of compensatory recruitment regulation (Fig. 6). The trajectories for juvenile haddock in years 1973 and 1981 are depicted by the dotted and dashed lines, respectively. Low adult abundance in 1973 resulted in faster juvenile growth (quadrant A) leading to larger adults in 1976 (quadrant B), higher recruitment in 1978 (quadrant C), and increased adult abundance in 1981 (quadrant D). Conversely, high adult abundance in 1981 reduced the growth of juvenile haddock (quadrant A) resulting in smaller-sized adults in 1984 (quadrant B), lower recruitment in 1986 (quadrant C), and decreased adult abundance in 1989 (quadrant D). The total time lag between application of the stress (adult abundance) and the feedback response (recruitment to age-4) is 8 years. However, this time lag could be decreased by 2 years if the total number of haddock age-3 and older were used as an index of adult abundance (quadrant A) and length at age-3 was used as the proxy for the reproductive potential of spawners (quadrants B and C).

Discussion

A significant, negative correlation between the length of juvenile haddock on the SWSS and adult abundance was observed for the time period covered by the CDN survey (1970–1995; Fig. 4A). Inverse correlations were not observed consistently through time (Fig. 4A versus Fig. 4B or Fig. 4C versus Fig. 4D) or space (e.g., SWSS versus BofF), which suggests that density-dependent growth is a weak effect and (or) that our ability to detect it is limited. The inverse correlation for the SWSS from 1970 to 1995 was consistent with the significant negative correlation observed between length at age-2 and total stock abundance for the Georges Bank haddock stock (Ross and Nelson 1992), which suggests that intercohort competition for food is characteristic of haddock. Spatial and dietary overlap between juveniles and adults is a pre-requisite for intercohort competition. High densities of age-1 haddock are typically found on offshore banks and stratum 90 (Marshall and Frank 1995), which also have high densities of adults (Frank et al. 1990). Juveniles feed on a size fraction of the macrobenthos that can also be utilized by adult haddock (Wildish et al. 1989). Databases describing interannual variation in food availability and (or) consumption would be required to examine intraspecific competition more directly.

From a population dynamics perspective, the density-dependent growth of juvenile haddock is of interest because it facilitates the compensatory recruitment regulation depicted in Fig. 6. Figure 6 applies only to time periods characterised by both density-dependent growth (Fig. 4A) and a positive correlation between recruitment and length at age-4 (fig. 6B in Marshall and Frank (1999)). When these two features of the stock dynamics are present, shifts towards either high abundance (e.g., because of anomalously high recruitment) or low abundance (e.g., because of high levels of fishing mortality) could induce cyclical variation in haddock recruitment at frequencies dependent on growth and maturation rates of the year-classes comprising the stock. Several stud-

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Table 3. Significance levels associated with sequential and partial sums of squares (SS) for models having length at age-1 as the dependent variable and adult abundance (total 4+) and (or) temperature (T) in either subarea 22 or subarea 24 as the independent variables.

Region	Time period	Independent variables	Sequential SS	Partial SS
SWSS	1970–1995	T (subarea 24)	0.52	0.29
SWSS	1963–1986	T (subarea 24)	0.28	0.53
BofF	1970–1995	T (subarea 22)	0.57	0.30
BofF	1963–1986	T (subarea 22)	0.02	0.21

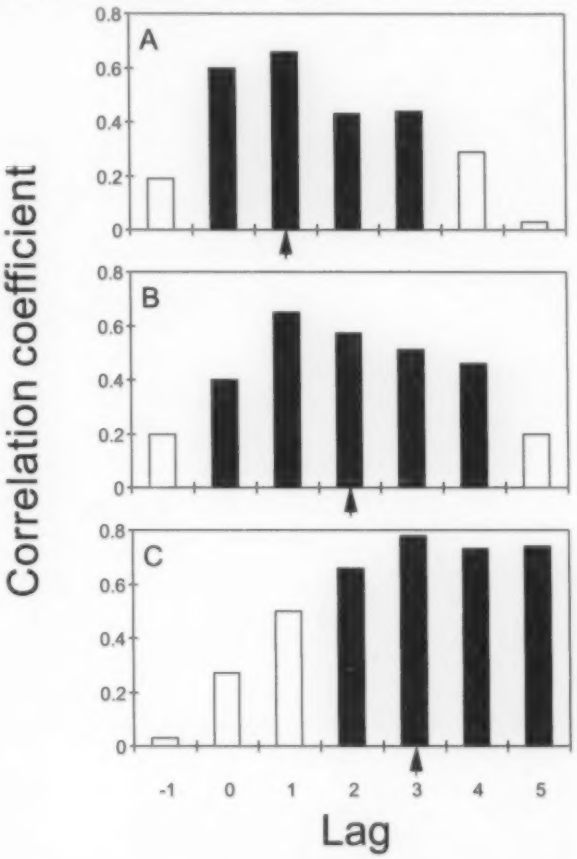
Note: The sequential SS were calculated assuming that T was the first variable to enter the model. The partial sums of squares were calculated for temperature assuming that adult abundance was already in the model.

ies have suggested that haddock exhibit cyclical variation in recruitment. For example, North Sea haddock have followed a 3- to 4-year cycle in recruitment throughout most of this century (Jones and Hislop 1978; Sahrhage and Wagner 1978) with very strong year-classes being frequently followed by very weak ones (Cook and Armstrong 1984). Hislop (1996) has suggested that this cyclical pattern originates in density-dependent mechanisms. The faster growth and maturation rates of North Sea haddock stock (age at 50% maturity is between 2 and 3 years; Cook and Armstrong 1984) would decrease the feedback time relative to SWSS haddock.

Although there are differences in both the processes and the time scales represented, the compensatory recruitment regulation model for haddock resembles the well-known Paulik diagram (Paulik 1973). The starting point for a Paulik diagram is the quadrant depicting the relationship between the quantity (or biomass) of spawners and total egg production. The Paulik diagram proceeds through time to describe the effect that mortality during egg and larval stages has on recruitment. The time lag between stock abundance and recruitment corresponds to the time taken to recruit (t_p). A Paulik diagram therefore describes the effect that the quantity of spawners has on recruitment via total egg production. Figure 6 describes the effect that the quantity of adults has on juvenile growth (quadrant A) and subsequently the effect that quality of spawners has on recruitment (quadrant C). The time lag is longer (approximately $2 \times t_p$) because two generations of haddock are represented in the model: the juveniles negatively impacted by adult abundance (the density-dependent effect) and the progeny produced by those juveniles once they mature (the maternal effect).

In the real world, the processes described by Fig. 6 and Paulik diagrams act in combination to determine recruitment. A conceptual model combining elements of both Fig. 6 and the Paulik diagram has been proposed to explain the recruitment dynamics of the Far Eastern sardine (*Sardinops sagax*) (fig. 5 in Kawasaki and Omori 1995). Like Fig. 6, this model incorporates both density-dependent and maternal effects on total egg production. Compensation occurs through the dependency of spawner condition on stock abundance; high stock abundance results in poor condition spawners and lower total egg production, which in turn reduces recruitment. Like a Paulik diagram, the survivorship of eggs was influenced by density-independent environmental processes.

Fig. 5. Cross correlation analysis for the southwestern Scotian Shelf (1970–1995). Arrows indicate the expected lag for a strong year-class effect. Solid bars indicate correlations significant at the $p^* \leq 0.05$ level, whereas open bars indicate correlations not significant. (A) Length at age-1 and age-2; (B) length at age-1 and age-3; (C) length at age-1 and age-4.



One of the earliest reported examples of density-dependent growth in haddock suggested that North Sea haddock compensate for low abundance by increasing growth rates thereby adjusting the "fertility" of the stock (Raitt 1939). Raitt (1936) presaged modern research on the effects of spawning experience on both egg viability (Solemdal et al. 1995) and population dynamics (Trippel et al. 1997*b*) by noting the potential for fishing mortality to remove repeat spawners from the population "forcing the brunt of recruitment upon two and three-year old fish much less well provided by nature to do so." This argues for the development of growth-based management strategies that consider both the current reproductive potential of adults and the short-term forecasts of growth and maturation rates of juveniles.

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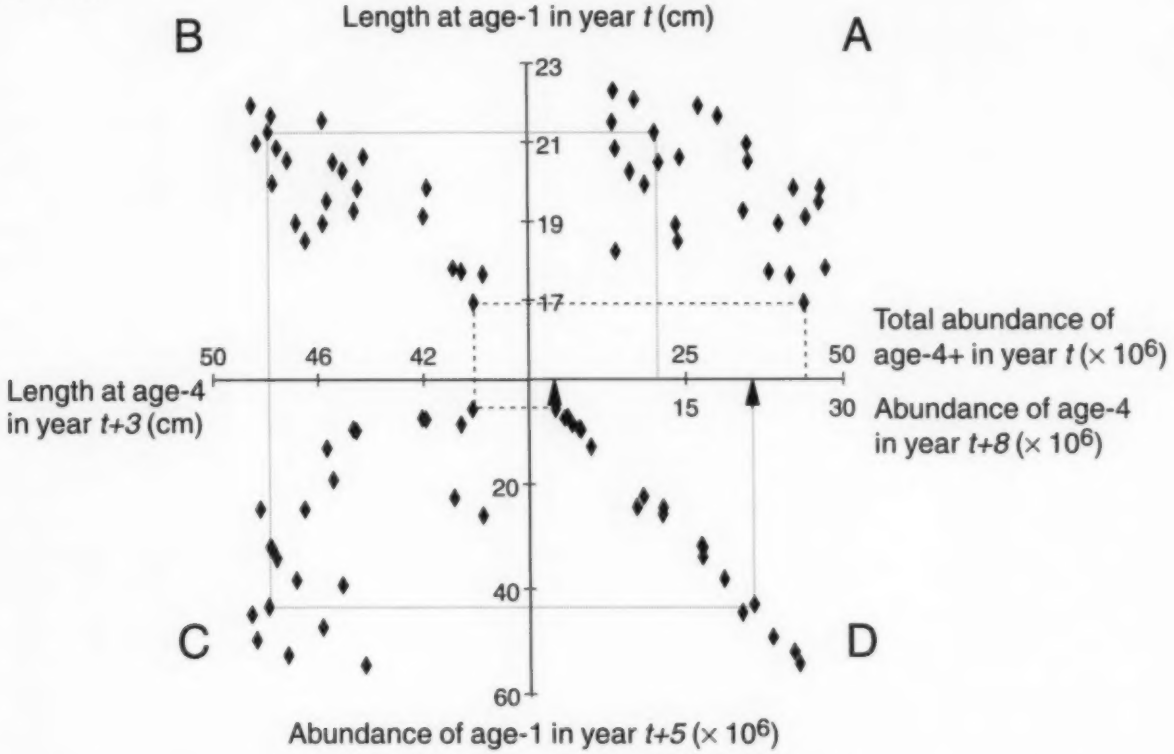
Fig. 6. A conceptual model for haddock on the southwestern Scotian Shelf illustrating compensatory responses in recruitment operating during the period 1970–1995. As in a Paulik diagram, the ordinate of one stage becomes the abscissa of the next, beginning here in the top right quadrant (quadrant A) and ending in the bottom right quadrant (quadrant D). The dotted line indicates the trajectory for t equal to 1973. The dashed line indicates the trajectory for t equal to 1981. Note the difference between the abscissa of quadrant A and the ordinate of quadrant D in both the magnitude (50 and 30 million, respectively) and the time scale (year t and year $t + 8$, respectively).



ments on earlier versions of this manuscript were provided by several anonymous referees and E.A. Trippel. Financial support was provided by scholarships from NSERC and the Killam Trust to C.T.M. and a NSERC research grant to K.T.F.

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Predator foraging mode shifts affecting mortality of juvenile fishes during the subarctic spring bloom

T.M. Willette, R.T. Cooney, and K. Hyer

Abstract: We examined some processes affecting foraging mode shifts among Pacific herring (*Clupea pallasi*) and walleye pollock (*Theragra chalcogramma*) during the spring bloom in Prince William Sound, Alaska. The duration of the bloom of the copepod *Neocalanus* was reduced when the surface layer became strongly stratified in May. Stronger surface layer stratification observed in 1995 and 1996 was associated with higher salinities below 50 m depth compared with 1994. Functional response models for Pacific herring and adult walleye pollock feeding on large calanoid copepods indicated that these predators began to switch to alternative prey as the mean biomass of large calanoid copepods declined below about 0.2 and 1.0 g/m^3, respectively. Analysis of covariance indicated that Pacific herring and walleye pollock tended to switch from large calanoid copepods to nekton prey after the copepod bloom declined ($p = 0.028$). Mortality of pink salmon (*Oncorhynchus gorbuscha*) was negatively correlated with the duration of the copepod bloom during the juvenile life stage ($p = 0.013$), as well as with juvenile growth rate ($p < 0.001$), juvenile body weight at release ($p < 0.001$), and the number of juveniles released ($p < 0.001$). Our results indicate that bottom-up processes affecting the duration of the spring bloom and juvenile growth also modify top-down processes involving foraging mode shifts toward piscivory and mortality of juvenile fishes.

Résumé : Nous avons examiné certains processus qui influent sur les changements alimentaires chez le hareng du Pacifique (*Clupea pallasi*) et la goberge de l'Alaska (*Theragra chalcogramma*) durant la prolifération printanière dans la baie Prince William, en Alaska. La durée de la prolifération des copépodes du genre *Neocalanus* était réduite quand la couche de surface devenait fortement stratifiée en mai. La stratification plus marquée de la couche de surface observée en 1995 et 1996 était associée à des salinités plus élevées qu'en 1994 sous les 50 premiers m. Les modèles fonctionnels de réponse pour le hareng du Pacifique et la goberge de l'Alaska adulte se nourrissant de gros copépodes calanoïdes ont montré que ces prédateurs ont commencé à se nourrir d'autres proies quand la biomasse moyenne des gros copépodes calanoïdes est passée sous la barre des 0,2 et 1,0 g/m^3, respectivement. L'analyse de covariance a montré que le hareng du Pacifique et la goberge de l'Alaska ont eu tendance à préférer les proies nectoniques aux gros copépodes calanoïdes après le déclin de la prolifération de copépodes ($p = 0{,}028$). La mortalité du saumon rose (*Oncorhynchus gorbuscha*) était corrélée négativement avec la durée de la prolifération de copépodes durant le stade juvénile ($p = 0{,}013$), de même qu'avec le taux de croissance des juvéniles ($p < 0{,}001$), le poids des juvéniles au moment du lâcher ($p < 0{,}001$) et le nombre de juvéniles lâchés ($p < 0{,}001$). Nos résultats montrent que les processus ascendants qui influent sur la durée de la prolifération printanière et la croissance des juvéniles modifient aussi les processus descendants impliquant le passage à une alimentation piscivore et la mortalité des poissons juvéniles.

[Traduit par la Rédaction]

Introduction

Trophic interactions during the spring plankton bloom are critical to the successful reproduction of many fish species that release larvae at this time. Mortality during these early life stages is typically very high and may determine recruitment to adult populations. Year class success may be determined by the match or mismatch between the release of larvae and the production of their food (Cushing 1967). This concept is based on the notion that recruitment success is driven by production from lower trophic levels (bottom up). However, these processes may be modified by interactions with animals at higher trophic levels (top down). Movements of the later life stages of subarctic fishes into the surface layer during this season lead to an overlap in distributions of larvae or juveniles with potential predators. Foraging mode shifts toward piscivory among these larger individuals may modify mortality rates of larval or juvenile life stages predicted by bottom-up processes.

In this paper, we evaluate the hypothesis that size-dependent mortality of larval and juvenile fishes is reduced during the spring bloom of large calanoid copepods because piscivory among the later life stages of Pacific herring (*Clupea pallasi*) and walleye pollock (*Theragra chalcogramma*) is reduced at this time. The later life stages of Pacific herring and walleye pollock are distributed in the

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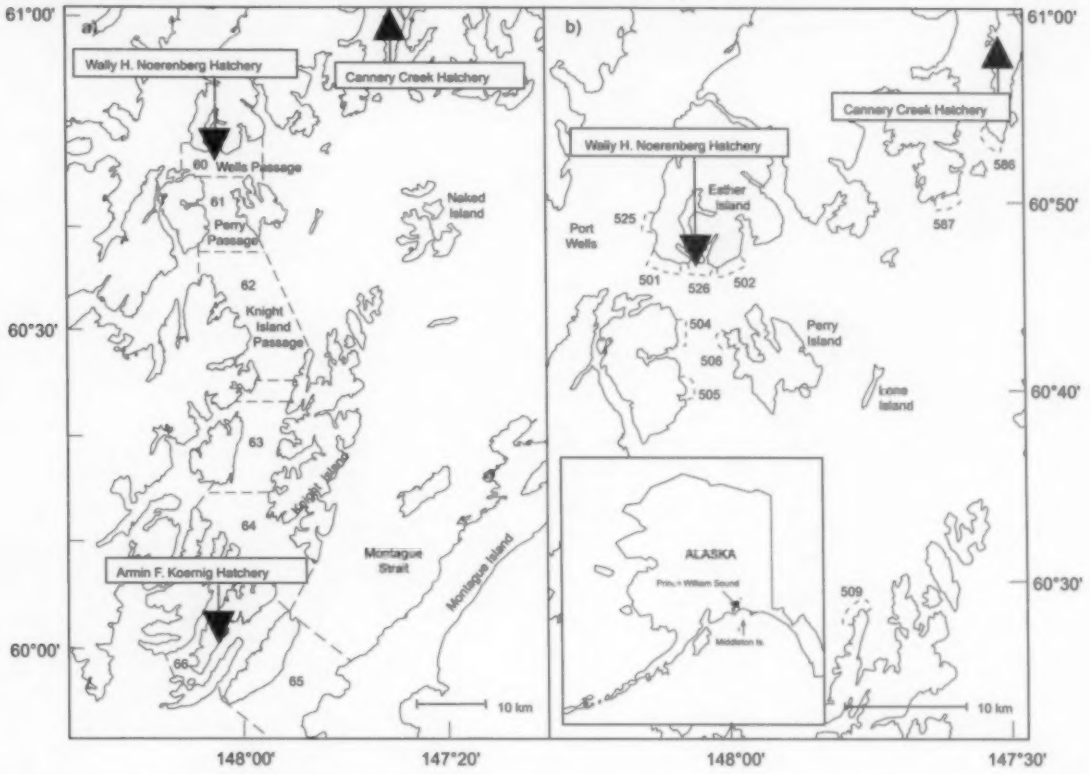
Fig. 1. Location of study areas in western Prince William Sound in (*a*) 1994 and (*b*) 1995 and 1996.



surface layers of the northern Gulf of Alaska during the spring bloom feeding heavily on large calanoid copepods (Coyle and Paul 1992; Yoshida 1994), but both species are also piscivorous (Thorsteinson 1962; Dwyer et al. 1987). The early life stages of Pacific herring, walleye pollock, pink salmon (*Oncorhynchus gorbuscha*), chum salmon (*Oncorhynchus keta*), capelin (*Mallotus villosus*), Pacific sand lance (*Ammodytes hexapterus*), and others enter the coastal ocean as larvae or juveniles during spring (Rogers et al. 1986). The copepods *Neocalanus plumchrus* and *Neocalanus flemingeri* (Miller 1988) compose the majority of the surface layer zooplankton biomass in the region during a brief period in late April and May (Cooney 1986). These large copepods build a substantial high-energy lipid reserve during the spring bloom that makes them an attractive food source for many fishes.

Particulate and filter feeding are common foraging modes employed by fish. Most optimal foraging models, developed for particulate-feeding planktivores, predict prey selection from the relative profitabilities of potential prey (Mittelbach 1981). Shifts between particulate and filter feeding are probably related to the relative profitability of each feeding strategy, which is largely determined by prey size and density (Crowder 1985). Durbin (1979) postulated that particulate feeders consume relatively large prey (prey–predator size ratio 0.5–5%), whereas filter feeders consume smaller prey (prey–predator size ratio 0.01–0.7%). Piscivory is a special case of particulate feeding (Breck 1993). Prey–predator size ratios typically range from 20 to 30% for piscivores, but ratios as high as 50% sometimes occur at ontogenetic transitions to piscivory (Popova 1978).

In the analysis that follows, we will first present data indicating seasonal changes in ocean conditions, calanoid copepod biomass, and the relative abundance and diet composition of Pacific herring and walleye pollock in Prince William Sound (PWS), Alaska. Three separate analyses will be conducted to evaluate our hypothesis. The functional responses of Pacific herring and walleye pollock feeding on large calanoid copepods will be estimated to determine the biomass of large calanoid copepods at which these predators switch to alternative prey or other foraging modes such as piscivory. We will then examine the prey–predator size ratios exhibited by each of these piscivores and test the hypothesis that piscivory is reduced when the biomass of large calanoid copepods is high. Finally, we will test the hypothesis that mortality of juvenile pink salmon is reduced when the duration of the bloom of large calanoid copepods is prolonged during the period from ocean entry to the time that juveniles reach 6 cm in length.

Methods

Field sampling and laboratory analyses

Pacific herring, walleye pollock, and their prey were sampled in several areas in western PWS from late April to mid July 1994 and from early May to mid-June 1995–1996 (Fig. 1). Sampling was conducted from about 18:00 to 06:00 the following morning from one to four times per month in each area. Samples aggregated by

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area and date formed "sample units". A midwater wing trawl (40 × 28 m) equipped with a net sounder was used to sample adult walleye pollock (>30 cm). The net was towed at about 1.5 m/s for about 30 min in the 0- to 60-m layer of the water column. At least two zooplankton samples were collected with a 0.5-m-diameter ring net (335-μm mesh) towed vertically from a depth of 50 m at midpassage stations in each area to estimate the density of large calanoid copepods available to adult walleye pollock. Pacific herring, immature walleye pollock (<30 cm), and various juvenile fishes were sampled with small-mesh purse seines (250 × 20 m, 1.5-cm stretch mesh) set in an approximate semicircle with the net open in the direction of the prevailing current for 20 min. Seine sampling was conducted within 1 km of the shore and up to the 20-m isobath. Pacific herring and immature walleye pollock were also sampled with variable-mesh gill nets set out from shore at two stations within each area. At least four zooplankton samples were taken in each area at stations located near the 20-m isobath to estimate the density of large calanoid copepods available to Pacific herring and immature walleye pollock in nearshore habitats. These samples were collected with a 0.5-m-diameter ring net (243-μm mesh) towed vertically from a depth of 20 m to the surface. In each study area, temperature and salinity were measured with a conductivity–temperature–depth (CTD) profiler to a depth of 100 m. Two hundred and nine trawl sets, 438 purse-seine sets, and 451 zooplankton casts were taken during the three years of the study.

The diet composition of Pacific herring and walleye pollock was estimated from specimens collected in 1994 (n = 4106), 1995 (n = 7342), and 1996 (n = 3958). At least 30 specimens from each fish species were randomly selected from each net set for stomach contents analysis. Fork length (FL) and wet weight were measured and stomachs excised and preserved in formalin for later analysis. In the laboratory, total stomach contents wet weight was measured, and the proportion of total stomach contents weight in several taxonomic groups (large calanoid copepods (>2.5 mm), small calanoid copepods (<2.5 mm), euphausiids and amphipods, and fish and squid) was visually estimated. Fish and squid found in the stomachs were measured to the nearest millimetre. Zooplankters collected with the 335-μm-mesh net were identified to the lowest possible taxonomic level and enumerated following standard subsampling techniques (Coyle et al. 1990). Zooplankters collected with the 243-μm-mesh net were enumerated into three taxonomic groups (large calanoid copepods, small calanoid copepods, and "other" zooplankton) using standard subsampling techniques. Zooplankton biomass was calculated as the product of abundance and the mean individual wet weight for each taxonomic group (Coyle et al. 1990).

The relative abundance of immature and adult fishes was examined through analyses of net catch data. Geometric mean catch per net set in small-mesh purse seines in each area was generally used as a measure of relative abundance (Hartt 1980), but geometric mean catch per hour in midwater trawls was used for adult walleye pollock. Analyses of variance were conducted to test for a difference in mean catch per net set between years for each taxonomic group. The mean proportion of the diet composed of various prey taxa, weighted by the catch of each predator in each net set, was estimated for Pacific herring, immature walleye pollock, and adult walleye pollock within each area. Analyses of variance were conducted to test for a difference in the mean proportion of the diet (arcsin square root transformed) composed of various prey taxa between May and June during each of the three years of the study.

Functional responses of Pacific herring and walleye pollock

The functional responses for Pacific herring, immature walleye pollock, and adult walleye pollock feeding on large calanoid copepods were evaluated using nonlinear regression analysis. Holling type II and III models were fit to field estimates of total daily consumption of large calanoid copepods in relation to measured copepod densities. Generally applying to particulate feeders, the type II functional response rises at a decelerating rate to an asymptote:

$$I = \frac{\gamma p U}{I + \gamma p U h}$$

where I is daily food consumption (grams per day), γ is the cross-sectional area of the reactive field (square metres), p is prey density (grams per cubic metre), U is swimming speed (metres per day), and h is prey handling time (grams per day). For ram filter feeders, γ is the cross-sectional area of the mouth gape because prey are not sighted and attacked. The model fit was evaluated for values of γ for particulate and filter feeding as well as swimming speeds ranging from 0.3 to 3.0 lengths/s. Because our analysis utilized field estimates of daily food consumption, swimming speed represented the total distance traversed while feeding throughout the day, and handling time included the time required to capture and ingest prey as well as any time during which the fish was not searching for prey due to satiation or low light level.

Daily comsumption of large calanoid copepods was estimated from $I = 24\bar{S}\alpha$, where $\bar{S}$ was the daily mean wet weight of large calanoid copepods in the stomach and α was the gastric evacuation rate (Eggers 1977). Stomach content data for the period from 18:00 to 06:00 the following morning were used in these calculations because data were available for this time period from each area and day. Analysis of variance indicated that the mean weight of copepods in the stomachs of these three predators was not significantly different ($p > 0.350$) between this 12-h period and the full 24-h day. Temperature-specific gastric evacuation rates were estimated for Pacific herring and walleye pollock using data provided by Peters and Kjelson (1975) and Smith et al. (1989).

The probable mean copepod biomass in plankton layers in the upper 50 m of the water column was used in our evaluation of functional responses of adult walleye pollock because adult walleye pollock were probably feeding in these high-density layers. Densities of large calanoid copepods within these layers were estimated from samples collected at 24 stations from eight discrete layers (0–5, 5–10, 10–15, 15–20, 20–25, 25–30, 30–40, and 40–50 m) in 1996 using a 1-m^2 multiple opening–closing net environmental sensing system. Samples having a copepod biomass greater than the mean for the upper 50 m as a whole were considered to have come from high-density layers. Regression analysis indicated that the mean biomass of large calanoid copepods in layers was about 2.25 times the biomass estimated from 0- to 50-m vertical net tows (R^2 = 0.451, df = 97, $p < 0.001$). For Pacific herring and immature walleye pollock feeding nearshore, we assumed that 0- to 20-m vertical net tows adequately estimated the mean biomass of copepods available in these shallow, tidally mixed habitats.

Nonlinear regression analyses were conducted in two stages using parameters for average-size Pacific herring (FL = 19.5 cm), immature walleye pollock (FL = 19.5 cm), and adult walleye pollock (FL = 50.1 cm). In the first stage, the fit of the models was evaluated using several possible values for handling time. Studentized-deleted residuals were calculated to identify and exclude outliers in the data at this stage (Neter et al. 1989). In the second stage, handling times estimated from the two best-fit models obtained in the first stage were used as constants to estimate U using the two values of γ associated with ram filter and particulate feeding. The value of γ that resulted in the best fit of the data was considered to indicate the probable feeding mode of the predator.

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Fig. 2. (*a*) Time series of sea level wind speed (2-day running mean), (*b*) ocean temperature (°C), (*c*) salinity (‰), and (*d*) the biomass of large calanoid copepods (dot-dashed line) and *Neocalanus* spp. (solid line) in the upper 50 m of the water column in Prince William Sound, 1994–1996. The dashed line in the third panel of Fig. 2*d* indicates the biomass of large calanoid copepods in the upper 20 m of the water column in nearshore habitats. The dotted line shown for wind speeds in 1995 is from Middleton Island (see Fig. 1).

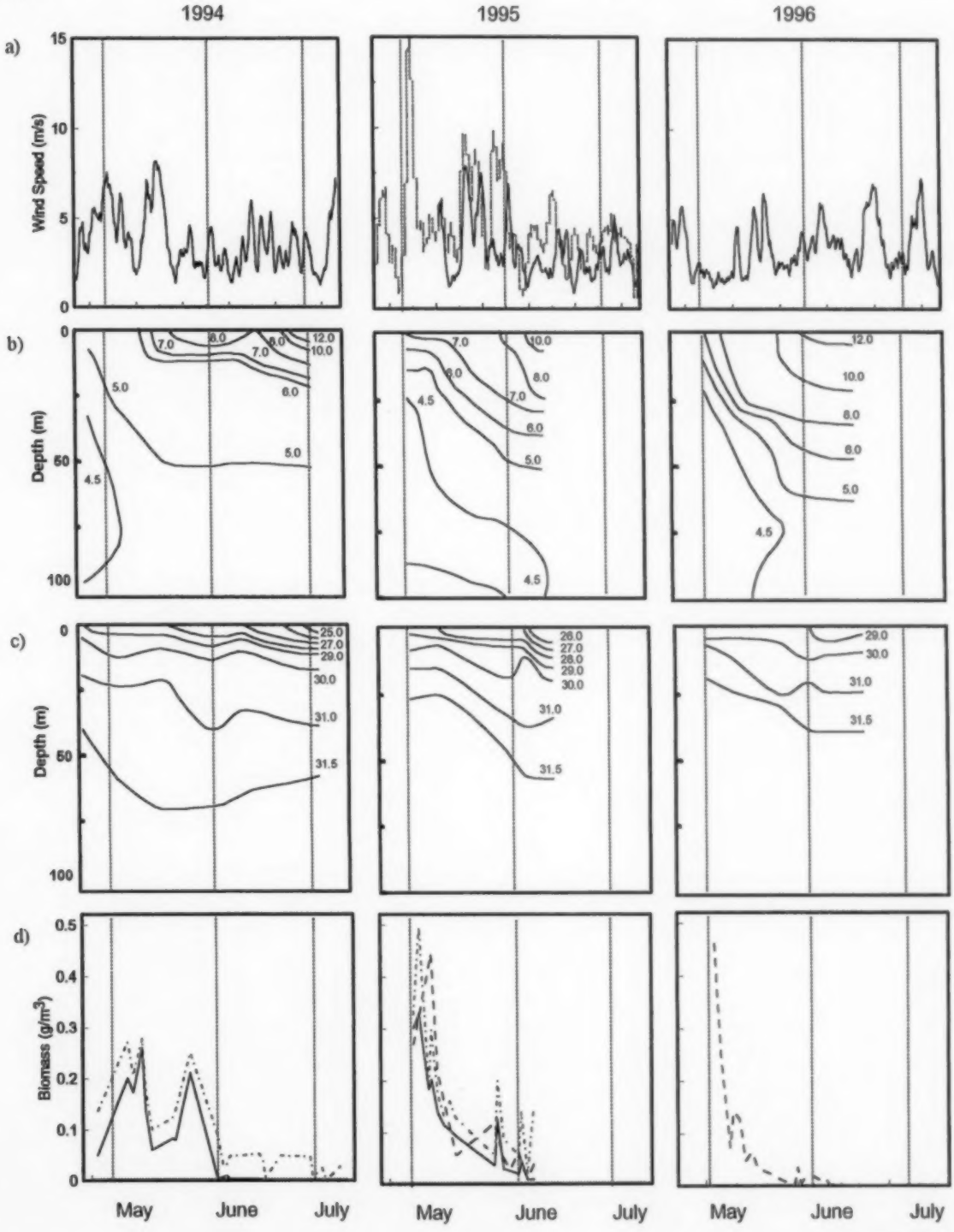

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Table 1. Geometric mean catch per net set for immature and adult fish and squid (>15 cm in length) in purse seines in western Prince William Sound, 1994–1996.

	Year			
Taxonomic group	1994	1995	1996	*p*
Pacific herring	6.52 (1.16)	10.52 (1.18)	3.11 (1.44)	0.005
Walleye pollock	31.16 (1.19)	33.44 (1.22)	13.60 (1.28)	0.009
Salmonids	1.69 (1.08)	1.61 (1.08)	1.53 (1.20)	0.827
Capelin	1.04 (1.04)	1.05 (1.04)	1.17 (1.09)	0.475
Pacific sand lance	1.01 (1.01)	1.01 (1.01)	0.00 (1.02)	0.880
Squid	1.13 (1.05)	1.17 (1.05)	4.76 (1.11)	<0.001
Other fish	1.16 (1.03)	1.43 (1.03)	1.11 (1.08)	<0.001

Note: Catch per hour of tow in midwater trawls is used for walleye pollock. The standard error of the mean is indicated in parentheses. Statistical test for a difference in mean catch per net set between years is indicated.

Piscivory among Pacific herring and walleye pollock

The mean percentage of the diet composed of nekton (fish and squid) in several taxonomic groups, weighted by the catch of each predator in each net set, was estimated for Pacific herring and immature and adult walleye pollock in each area. Squid were included in this analysis because they composed a substantial proportion of the nekton in adult walleye pollock diets. Geometric mean catch per net set in purse seines and mean length were also estimated for each of the taxonomic groups of potential nekton prey (<15 cm FL). Analyses of variance were conducted to test for differences in the mean proportion of the diet (arcsin square root transformed) composed of the various nekton prey for each predator within each year as well as differences in the geometric mean catch per net set among potential nekton prey within each year. Regression analyses were conducted to test for changes in mean length of potential nekton prey during the spring bloom with data from all years pooled. Prey–predator length ratios were calculated for Pacific herring (n = 634), immature walleye pollock (n = 436), and adult walleye pollock (n = 820) with all nekton prey pooled and for the four dominant groups of nekton prey in the diets of the three predators. Analyses of variance were conducted to test for differences in the mean prey–predator length ratio (arcsin square root transformed) among the three predators and among the four groups of nekton in the diet of each predator.

An analysis of covariance was conducted to test the hypothesis that piscivory in Pacific herring and walleye pollock was reduced when the biomass of large calanoid copepods was high. The mean proportion of the diet composed of nekton (arcsin square root transformed) in each area was the dependent variable in the analysis. The geometric mean catch per net set of potential nekton prey in purse seines and the mean biomass of large calanoid copepods in each area were the independent variables. A stepwise procedure was used to develop the most parsimonious model. The variance inflation factor was calculated to assess whether multicollinearity may have affected estimation of the regression coefficients and their statistical significance (Neter et al. 1989).

Calanoid copepod biomass and mortality of juvenile salmonids

An analysis of covariance was conducted to test the hypothesis that mortality of juvenile pink salmon was reduced when the duration of the bloom of large calanoid copepods was prolonged during the period from ocean entry to the time that juveniles reach 6 cm FL. Estimates of instantaneous natural mortality from ocean entry to adult (Geiger 1990) for 147 coded-wire tag (CWT) groups of pink salmon released from the Armin F. Koernig, Wally H. Noerenberg, Cannery Creek, and Solomon Gulch hatcheries (1989–1995) were used as the dependent variable in the analysis. A CWT group was composed of one or more net pens of juveniles released from the same hatchery on the same day. Mean zooplankton settled volume, mean juvenile body weight at release, mean juvenile growth rate, and number of juveniles in each CWT group were the independent variables. A stepwise analysis of covariance procedure was used to develop the most parsimonious model of mortality.

Mean zooplankton settled volume, weighted by the number of days elapsed between each measurement, was estimated for the 30 days immediately following release of each CWT group. We selected 30 days because sampling of tagged juveniles indicated that 98.5% of the fish did not reach 6 cm FL within 30 days after release. Zooplankton settled volume was estimated from one to three samples collected twice each week using a 0.5-m-diameter ring net (243-μm mesh) towed vertically from 20 m to the surface in the passages adjacent to each hatchery. The volume of zooplankton in the pooled samples was estimated in a graduated cylinder after the material had settled. Zooplankton volumes greater than 2.0 mL/m^3 were set equal to 2.0 mL/m^3 because predator stomach content analyses indicated that the relationship between copepod biomass and consumption of fish was nonlinear, with piscivory reduced above this threshold. Data from Willette et al. (1994) and the present study indicated that zooplankton settled volume was correlated with large calanoid copepod biomass in May (R^2 = 0.660, df = 38, p < 0.001) and that our threshold settled volume was approximately equal to a large calanoid copepod biomass of 0.2 g/m^3. A class variable was established based on the value of the mean zooplankton settled volume (millilitres per cubic metre) that divided the data into three groups with roughly equal numbers of observations: low, 1.3 (n = 50); moderate, 1.9 (n = 56); high, 2.0 (n = 48). Mean body weight of juvenile salmon at release was estimated from three samples collected from each net pen immediately prior to release. Tag groups composed of larger fish at release (0.35–1.3 g) were not included in the analysis because they were relatively rare (<9% of the data) and occurred more frequently in association with the moderate and high zooplankton classes.

The mean growth rates of the 147 CWT groups in our analysis were estimated from a function relating juvenile growth to environmental and juvenile release data. The function was developed using growth rate estimates for 2637 individual CWT juvenile pink salmon collected (Willette et al. 1994) during May and early June in PWS (1989–1994). The dependent variable was mean juvenile growth, and the independent variables were mean zooplankton volume, mean ocean temperature, and number of juveniles released. Mean growth was estimated for juveniles that exhibited a common release site, release date, and recapture date. Mean zooplankton settled volumes and ocean temperatures, weighted by the number of days between each measurement, were estimated from the date of release of each CWT group to the date of recapture. Ocean temperatures were measured at 1 m depth when zooplankton samples were collected. A class variable was established based on the number of juveniles released each day from each hatchery that divided

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Fig. 3. Mean percentage of the diet composed of large copepods, pteropods, euphausiids and amphipods, and nekton (fish and squid) for Pacific herring, immature walleye pollock, and adult walleye pollock in western Prince William Sound during 1994 (solid squares), 1995 (solid circles), and 1996 (open circles).

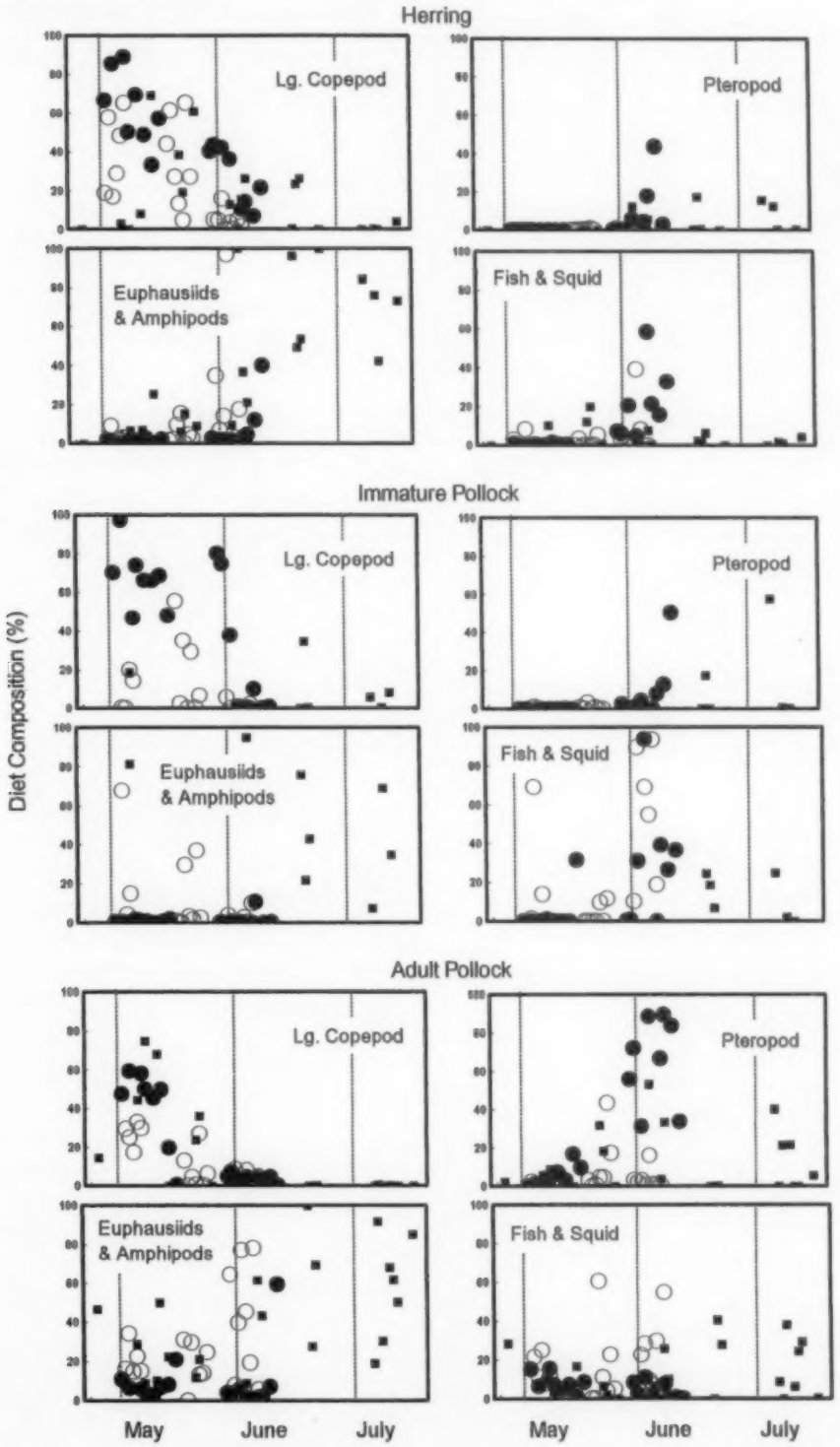

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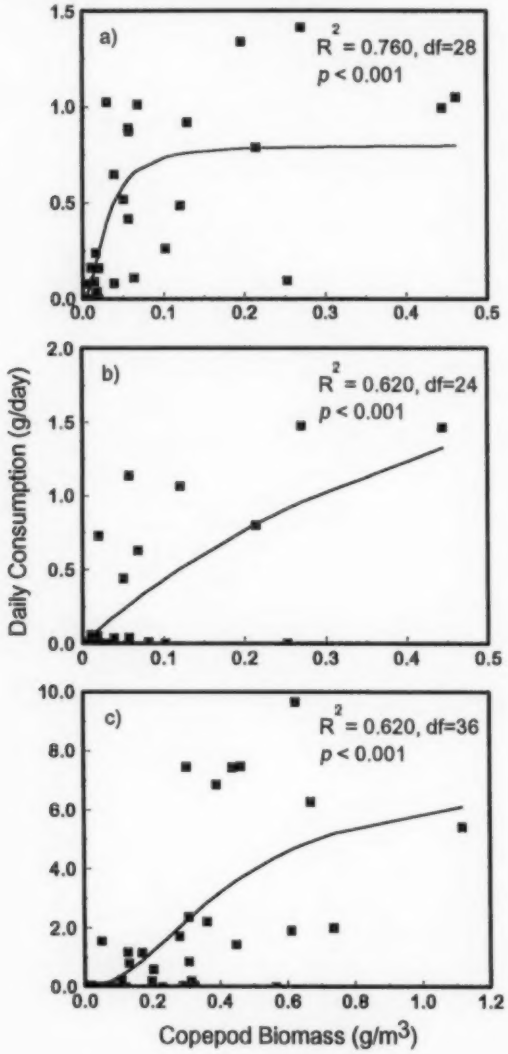
Fig. 4. Best-fit functional response models for (*a*) Pacific herring, (*b*) immature walleye pollock, and (*c*) adult walleye pollock feeding on large calanoid copepods.



the data into two groups with roughly equal numbers of observations. Groups with <20 million juveniles were designated as small and those with >20 million as large. A stepwise analysis of covariance procedure was used to develop the most parsimonious model of juvenile growth.

Results

Relatively frequent storms, weak surface layer stratification, cooler surface layer temperatures, and a prolonged bloom of large calanoid copepods characterized ocean conditions in May 1994 (Fig. 2). In May 1995, storms were again frequent in the area, but the water column was more strongly stratified than in 1994, surface temperatures were warmer, and the bloom of large calanoid copepods was more abbreviated. In May 1996, storms were less frequent, the water column was again strongly stratified, surface layer temperatures were relatively warm, and the bloom of large calanoid copepods was very abbreviated. In each of the three years of this study, the surface layer became strongly stratified in June and the bloom of large calanoid copepods declined. The biomass of large calanoid copepods was composed primarily of *Neocalanus* in both 1994 and 1995 (Fig. 2).

Pacific herring and walleye pollock were the most abundant pelagic fishes during each of the three years of this study, but squid (mostly *Berryteuthis* spp.) were relatively abundant in 1996 (Table 1). Pacific herring abundance was significantly higher in 1995 and walleye pollock abundance lower in 1996 compared with the other years of the study (Table 1). Large calanoid copepods composed a significantly greater ($p < 0.001$) proportion of the diets of Pacific herring, immature walleye pollock, and adult walleye pollock during May than during June 1994–1996 (Fig. 3). In all three years of the study, Pacific herring and immature and adult walleye pollock switched to feeding on alternative prey during June. In 1994, the proportion of Pacific herring and adult walleye pollock diets composed of euphausiids and amphipods increased significantly during June ($p < 0.001$). In 1995, the proportion of Pacific herring and immature walleye pollock diets composed of pteropods and fish increased significantly during June ($p < 0.001$), whereas among adult walleye pollock, only consumption of pteropods increased during June ($p < 0.001$). In 1996, the proportion of the diet composed of fish increased significantly during June among Pacific herring ($p = 0.034$) and immature walleye pollock ($p < 0.001$) but not adult walleye pollock.

Functional responses of Pacific herring and walleye pollock

Type III models best described the functional responses of Pacific herring and adult walleye pollock feeding on large calanoid copepods (Fig. 4). Type II or III models did not adequately describe the functional response of immature walleye pollock because the function did not reach an asymptote within the range of the data. Studentized-deleted residuals identified two outliers that were excluded from the analysis for Pacific herring. Values of γ consistent with particulate and ram filter feeding modes provided the best fit of the Pacific herring and adult walleye pollock data, respectively, at all values of swimming speed used in the analysis. The best-fit models for Pacific herring and adult walleye pollock resulted in swimming speed estimates of 10.0 and 16.7 km/day and daily food consumption estimates of 0.8 and 7.0 g/day at the asymptote, respectively. Pacific herring began to feed on alternative prey as the mean biomass of large calanoid copepods in the upper 20 m of the water column declined below about 0.2 g/m^3. Adult walleye pollock began to feed on alternative prey as the mean biomass of large calanoid copepods in high-density layers declined below about 1.0 g/m^3.

Piscivory among Pacific herring and walleye pollock

Immature walleye pollock generally exhibited a greater degree of piscivory than either Pacific herring or adult walleye pollock: 4.2–11.4% nekton for Pacific herring, 13.9–26.2% nekton for immature walleye pollock, and

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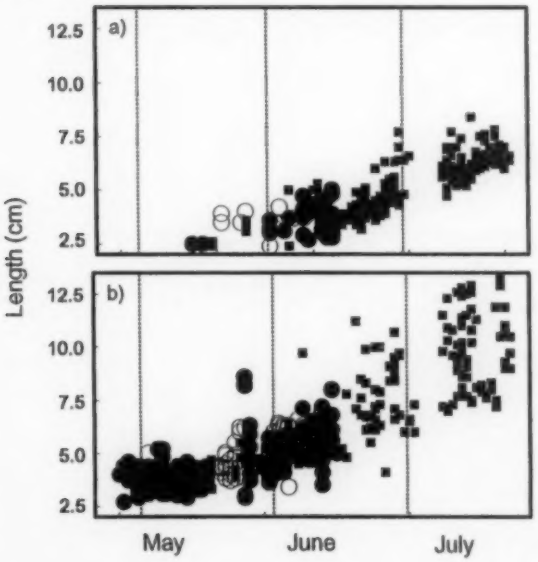
Table 2. Geometric mean catch per net set for potential nekton prey (<15 cm in length) in purse seines and mean percentage of the diet for various nekton prey consumed by Pacific herring, immature walleye pollock, and adult walleye pollock in western Prince William Sound, 1994–1996.

			Diet composition (%)		
Year	Prey	Mean catch	Pacific herring	Immature walleye pollock	Adult walleye pollock
1994	Pacific herring	1.66 (1.08)	0.12 (0.37)	0.01 (0.70)	0.91 (0.36)
	Gadids	**54.60** (1.21)	**0.39** (0.98)	**3.42** (1.83)	2.16 (0.93)
	Salmonids	**5.40** (1.13)	0.04 (0.23)	0.03 (0.43)	0.94 (0.22)
	Capelin	1.18 (1.04)	0	0	0
	Pacific sand lance	1.04 (1.02)	0.11 (0.09)	0	0.16 (0.09)
	Squid	1.03 (1.01)	0	0	**4.90** (0.93)
	Other fish	1.57 (1.05)	0.14 (0.77)	0.22 (1.44)	2.22 (0.73)
	Total nekton	165.50 (1.15)	4.44 (2.14)	14.43 (4.01)	17.06 (2.04)
1995	Pacific herring	1.57 (1.08)	0	0	0.11 (0.04)
	Gadids	1.33 (1.08)	1.13 (0.73)	2.03 (1.01)	0.30 (0.72)
	Salmonids	**3.72** (1.16)	0.09 (0.66)	4.08 (0.91)	0.13 (0.65)
	Capelin	2.13 (1.08)	0	0	0
	Pacific sand lance	1.03 (1.01)	0	0	0
	Squid	1.62 (1.07)	0.01 (0.44)	0	**3.81** (0.44)
	Other fish	**3.07** (1.11)	0.31 (0.22)	0.67 (0.31)	0.14 (0.22)
	Total nekton	22.13 (1.14)	11.39 (1.91)	13.90 (2.64)	6.69 (1.88)
1996	Pacific herring	1.13 (1.07)	0	0	1.69 (0.72)
	Gadids	1.53 (1.22)	0.05 (0.03)	0	0.01 (0.03)
	Salmonids	**27.58** (1.53)	**3.18** (1.81)	10.32 (2.43)	1.10 (1.84)
	Capelin	2.44 (1.20)	0	0	0.73 (0.45)
	Pacific sand lance	0	0	7.23 (1.90)	0
	Squid	3.50 (1.30)	0	0	**7.67** (1.39)
	Other fish	2.44 (1.24)	0.35 (0.33)	1.38 (0.44)	0.27 (0.33)
	Total nekton	104.48 (1.32)	4.18 (2.86)	26.25 (3.83)	16.02 (2.90)

Note: Total nekton prey includes unidentified fish or squid. Within each column and year, means indicated in bold are significantly greater ($p < 0.050$) than means that are not in bold. The standard error of the mean is indicated in parentheses.

Fig. 5. Mean lengths of juvenile (*a*) gadids and (*b*) salmonids in small-mesh purse seines in nearshore habitats of western Prince William Sound during 1994 (solid squares), 1995 (solid circles), and 1996 (open circles).



6.7–17.1% nekton for adult walleye pollock (Table 2). Juvenile gadids (mostly age-0 walleye pollock) and salmonids (mostly pink and chum salmon) generally composed the greatest proportion of the nekton prey of Pacific herring and immature walleye pollock, whereas squid was the most important nekton in the diets of adult walleye pollock. Gadids and salmonids in 1994, salmonids and other nekton in 1995, and salmonids in 1996 dominated catches of potential nekton prey in purse seines (Table 2). Mean lengths of juvenile gadids and salmonids (Fig. 5) increased 1.1 and 1.6%/day ($p < 0.001$), whereas mean lengths of other nekton taxa ranged from 5 to 25 cm and changed less than 0.6%/day.

Pacific herring and immature walleye pollock generally consumed nekton less than 6 cm in length, whereas adult walleye pollock consumed nekton less than 15 cm in length (Fig. 6). Mean prey lengths and prey–predator length ratios were significantly different ($p < 0.001$) among the three predators with all prey taxa pooled. Mean prey lengths and prey–predator length ratios were also significantly different among the four dominant prey taxa for Pacific herring ($p < 0.001$), immature walleye pollock ($p = 0.056$), and adult walleye pollock ($p < 0.001$).

The proportion of Pacific herring and walleye pollock diets composed of nekton was significantly negatively correlated with the biomass of large calanoid copepods (Table 3; Fig. 7). The term in the model indicating an interaction between copepod biomass and predator taxonomic group was removed because it was not significant ($p = 0.397$). The

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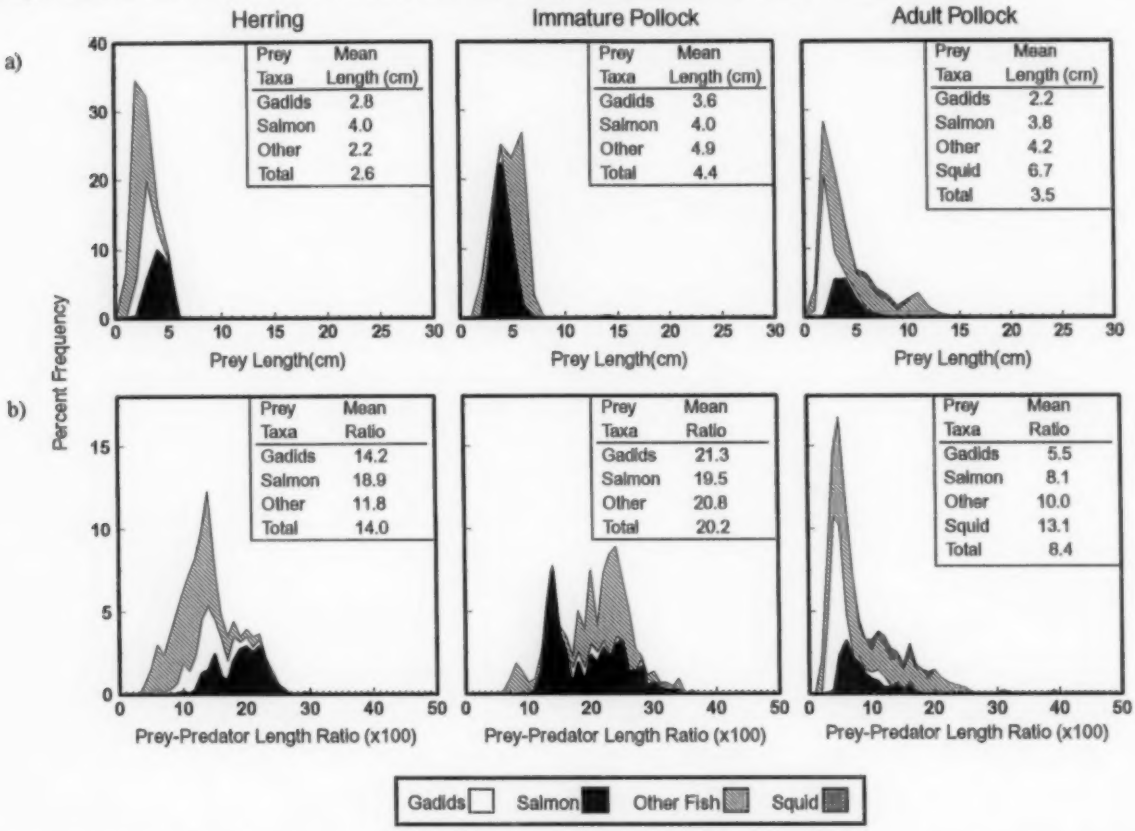
Fig. 6. (*a*) Length frequency and mean lengths and (*b*) prey–predator length ratios and mean ratios for salmonids, gadids, other fish, and squid found in the stomachs of Pacific herring, immature walleye pollock, and adult walleye pollock, 1994–1996.



slope of the relationship between the proportion of the diet composed of nekton and the relative abundance of potential nekton prey was significantly different from zero ($p = 0.002$) for immature walleye pollock but not for the other predators. Graphical evaluation of the original data indicated that the proportion of predator diets composed of nekton tended to be greater when the biomass of large copepods was less than about 0.2 g/m^3 (Fig. 7). The variance inflation factor for this analysis was 3.12.

Calanoid copepod biomass and mortality of juvenile salmonids

Analysis of covariance indicated that the growth rate of CWT juvenile pink salmon was positively correlated with mean ocean temperature ($p = 0.002$) and zooplankton settled volume ($p < 0.001$) during the period from juvenile release to recapture ($R^2 = 0.474$, df = 107, $p < 0.001$). The slope of the relationship between growth and zooplankton settled volume was also significantly different ($p < 0.001$) between small and large release groups, indicating a reduction in growth for individuals in large release groups during periods of low zooplankton density. The variance inflation factor for this analysis was 4.60.

The instantaneous natural mortality of pink salmon was significantly negatively correlated (Table 4) with mean zooplankton settled volume during the initial 30 days of marine residence, mean juvenile growth rate, mean body weight of juveniles at release, and number of juveniles released ($R^2 = 0.350$, df = 146, $p < 0.001$). The variance inflation factor for this analysis was 6.54.

Discussion

The environmental conditions observed during this 3-year study provided for a useful comparison of the effect of physical conditions on secondary production in the PWS ecosystem. The duration of the bloom of large calanoid copepods in May appeared to be associated with the degree of stratification of the surface layer. In 1994, the surface layer was weakly stratified, and the bloom of large copepods extended to the end of May (Fig. 2). In May 1995 and 1996, the surface layer was more highly stratified, and the bloom of large copepods was more abbreviated. These associations were probably related to the frequency of storms with winds sufficiently strong to disrupt surface stratification, resupply nutrients to the surface mixed layer, and thus prolong the phytoplankton bloom (Iverson et al. 1974). In years when storms were more frequent and the phytoplankton bloom was prolonged, the mean (April–June) abundance and growth of *N. plumchrus* were greater (Sambrotto and

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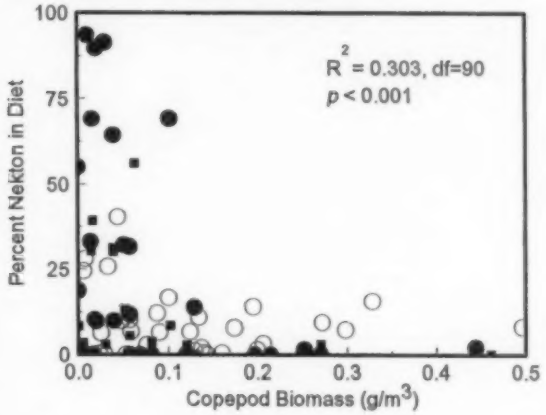
Table 3. Parameters estimated from an analysis of covariance.

Parameter	Estimate	Least squares mean	SE	p
Intercept	0.3709	—	0.1063	0.001
Predator taxonomic group				
Pacific herring	–0.1887	0.1912	0.0506	0.079
Immature walleye pollock	–0.3848	0.3966	0.0529	—
Adult walleye pollock	0.0000	0.2537	0.0524	—
Relative abundance nekton prey	–0.0153	—	0.0292	0.124
Calanoid copepod biomass	–0.5956	—	0.2666	0.028
Prey abundance × predator				
Pacific herring	–0.0122	—	0.0416	0.002
Immature walleye pollock	0.1478	—	0.0461	—
Adult walleye pollock	0.0000	—	—	—

Note: The proportion of Pacific herring and walleye pollock diets composed of nekton was the dependent variable. The relative abundance of potential nekton prey and the biomass of large calanoid copepods were the independent variables.

Fig. 7. Relationship between the mean percentage of the diet composed of nekton and the biomass of large calanoid copepods for Pacific herring (solid squares), immature walleye pollock (solid circles), and adult walleye pollock (open circles), 1994–1996.



Goering 1983). The frequency of wind events was similar during May in 1994 and 1995 (Fig. 2), yet the surface layer remained more highly stratified in 1995. This indicated that other physical processes that affect development of surface stratification probably modified the effect of intense storms on primary and secondary production. The stronger surface layer stratification observed in May 1995 and 1996 was associated with higher salinities and lower temperatures below 50 m depth compared with 1994 (Fig. 2). The strength of surface stratification during this season is largely determined by the vertical salinity gradient because seawater density is primarily a function of salinity at low temperature (Royer 1979). Thus, in years when the 0- to 100-m salinity is relatively high at the onset of the spring bloom, the seasonal decrease in surface salinity due to increased freshwater discharge (Xiong and Royer 1984) results in a greater vertical salinity (density) gradient compared with years when the 0- to 100-m salinity is relatively low at the onset of the spring bloom. Higher wind speeds are required to break down the stronger surface stratification that occurs under these conditions. Thus, it appears that the relatively high wind speeds that occurred in May 1995 were insufficient to disrupt the relatively strong surface stratification, so the bloom of large calanoid copepods was more abbreviated.

Large-scale oceanographic processes occurring the previous winter may determine the 0- to 100-m temperature–salinity conditions present at the onset of the spring bloom. Lower ocean temperatures and sea levels in the northeastern Pacific are associated with a weaker winter Aleutian low (Emery and Hamilton 1985). Higher salinities in this region are associated with reduced freshwater discharge (Xiong and Royer 1984), and lower sea levels are associated with reduced precipitation and dynamic height of the upper layers of the ocean (Royer 1979). Thus, a weak (strong) Aleutian low during the previous winter probably results in relatively high (low) 0- to 100-m salinities and low (high) 0- to 100-m temperatures at the onset of the spring bloom. Niebauer et al. (1994) concluded that 200% of the volume of PWS is flushed during winter (October–April) and that flushing of the surface layer (0–100 m) is most rapid during winter. Thus, large-scale oceanographic processes in the Gulf of Alaska may be expected to affect conditions in the surface layer of PWS during winter.

Determining the appropriate functional response model for specific predator–prey interactions has often proved difficult. We recognize that Pacific herring and walleye pollock probably feed in high-density patches or layers of copepods because relatively mobile predators often aggregate in areas where relatively immobile invertebrate prey occur at high densities (Krebs 1973). Our analysis was based on the assumption that relatively large-scale seasonal changes in mean surface layer copepod densities were correlated with densities in patches exploited by Pacific herring and walleye pollock. The validity of this assumption is supported by the fact that our method for estimating daily consumption of copepods probably integrated amounts taken from many patches by many individuals over a 12-h period.

A sigmoid type III functional response model provided the best fit of our Pacific herring and adult walleye pollock data. The parameters of our best-fit response model for Pacific herring were consistent with a particulate-feeding mode. An identical fit could have been obtained with values for γ of 0.0001 m^2 (consistent with ram filter feeding) and U of 469 lengths/s, but this swimming speed was not physiologically possible. Filter feeding is energetically more profitable than

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Table 4. Parameters estimated from an analysis of covariance. The instantaneous natural mortality of coded-wire-tagged pink salmon was the dependent variable.

Parameter	Estimate	Least squares mean	SE	*p*
Intercept	0.0774	—	0.0123	<0.001
Zooplankton volume				
Low	0.0014	0.0097	0.0006	0.013
Moderate	0.0002	0.0085	0.0005	—
High	0.0000	0.0083	—	—
Mean juvenile growth rate	–0.0112	—	0.0024	<0.001
Body weight at release	–0.2419	—	0.0455	<0.001
Number juveniles released	–0.0077	—	0.0020	<0.001
Growth × release weight	0.0391	—	0.0085	<0.001
Number released × release weight	0.0264	—	0.0075	<0.001

Note: Mean zooplankton settled volume during the initial 30 days of marine residence, mean juvenile pink salmon growth rate, mean body weight at release, and number of juveniles released from each hatchery each day were the independent variables.

particulate feeding for Pacific herring (13–20 cm) feeding on *Calanus finmarchichus* (2.8 mm) at prey densities exceeding about 13 000 individuals/m^3 (Gibson and Ezzi 1992). In the present study, densities of large calanoid copepods were only 80 individuals/m^3 at the asymptote of our functional response model for Pacific herring. Our estimated mean copepod density in layers was about 385 individuals/m^3 at the asymptote of our best-fit response model for adult walleye pollock. No laboratory data were available regarding the densities required for fish the size of adult walleye pollock to profitably filter feed on prey the size of large calanoid copepods. The swimming speed estimated from our best-fit response model for adult walleye pollock was very similar to that estimated from field measurements of foraging schools of adult walleye pollock in the Bering Sea (Radchenko and Sobolevskiy 1993).

The parameters of our best-fit functional response model for adult walleye pollock were consistent with a ram filter feeding mode and daily food consumption limited by gastric evacuation. Ram filtering involves continuous swimming with the mouth agape and opercles flared (Gerking 1994). As previously indicated, our handling time estimate included time spent capturing and ingesting prey as well as any time not spent searching for prey due to satiation or low light level. The daily food consumption at the asymptote of our functional response model for adult walleye pollock was equivalent to 0.08 mg/s at a prey density of 1.0 g/m^3. If we assumed continuous feeding throughout the day and no limitation due to gastric evacuation rate, an adult walleye pollock swimming at 0.2 m/s filter feeding on copepods at a density of 1.0 g/m^3 should have consumed prey at a rate of about 0.4 mg/s. If adult walleye pollock were filter feeding, low light level would not limit the time spent feeding, indicating that gastric evacuation rate probably limited daily food consumption.

Our estimated mean prey–predator length ratios for Pacific herring and adult walleye pollock were below the mean prey–predator length ratios of 20–30% typically observed among piscivorous fish. Minimum and modal prey lengths were similar for both immature and adult walleye pollock, but adult walleye pollock consumed prey up to 15 cm, which were not taken by immature walleye pollock (Fig. 6). In a review of piscivory in freshwater systems, Popova (1978) found that maximum prey size increased as predaceous fish grew, whereas minimum prey size remained constant. Thus, mean prey–predator length ratios tended to stabilize around 10% for larger predators. Our results are generally consistent with Popova's (1978) conclusions, suggesting that similar generalizations apply in marine systems. Our analysis also indicated significant differences in mean prey–predator length ratios among the four dominant nekton prey taxa for each predator. However, the magnitude of the differences was generally small and appeared to be related to the sizes of available prey.

Our analyses indicated that Pacific herring and walleye pollock tended to switch from large calanoid copepods to nekton prey after the decline of the copepod bloom (Table 3). Pacific herring and walleye pollock diets were generally dominated by large calanoid copepods during the bloom in May (Fig. 3). After the copepod bloom, Pacific herring and walleye pollock tended to consume more nekton, but other alternative prey were also taken (Fig. 3). Juvenile gadids and salmonids were the most commonly encountered fish in the diets of Pacific herring and immature walleye pollock, whereas squid were commonly encountered in the diets of adult walleye pollock (Table 2). Thus, as Pacific herring and walleye pollock switched to feeding on fish and squid after the copepod bloom, mortality among these animals probably increased.

CWT data allowed us to further examine whether mortality among juvenile pink salmon was related to copepod biomass. The analysis was structured to enable examination of the simultaneous effects of zooplankton density on juvenile growth rate and predator switching behavior. The results from this analysis supported the hypothesis that a prolonged spring bloom of large calanoid copepods generally resulted in reduced mortality among juvenile pelagic fishes (Table 4). This result was also generally consistent with our analyses of predator stomach contents (Table 3; Fig. 7), suggesting that predator switching behavior was the cause.

In our study, mortality of hatchery-reared pink salmon during the marine life stage appeared to be depensatory. We cannot conclusively determine the processes that caused the observed depensation, but saturation of predator populations feeding on juvenile salmon was a possible cause. Data presented by Dobrynina et al. (1989) indicated that several marine fish species feeding on juvenile pink salmon emigrating from the Utka River were probably operating near the lower

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end of their functional response curves. But the densities of juveniles in this natural setting were probably much lower than those resulting from large-scale releases of hatchery-reared fish.

Mortality among juvenile salmonids is probably affected by the timing of the seasonal decline of the *Neocalanus* bloom relative to the prey fishes' growth rate. The mortality of other larval or relatively small juvenile fishes (gadids, Pacific sand lance, capelin, Pacific herring, etc.) that occur in pelagic habitats during the spring bloom is probably also affected by these processes. In our study, juvenile salmonids were growing rapidly at this time of year (Fig. 5). Modal lengths of juvenile salmon in Pacific herring and walleye pollock stomachs were about 4 cm FL, and individuals greater than 6 cm FL were rare (Fig. 6). These data are consistent with Healey's (1982) conclusion that mortality among juvenile chum salmon is highly size selective between 4.5 and 5.5 cm FL when these fish migrate into pelagic habitats. Healey (1982) was unable to determine the magnitude of predation during this life stage, but our results suggest that it may be relatively high (Fig. 3). Juvenile salmon in PWS typically migrated into pelagic habitats in early June. We observed relatively high predation rates on juvenile fish in early June in some years (Fig. 3). This probably occurred because copepod densities had generally declined by this time (Fig. 2), yet a substantial proportion of the juvenile gadid and salmonid population was still vulnerable to predation due to their small size (Fig. 5).

Thus, bottom-up processes may affect mortality of juvenile fishes during the spring bloom through effects of temperature and zooplankton density on juvenile growth rate. However, these bottom-up effects probably also modify top-down processes involving the timing of feeding mode shifts toward piscivory among the later life stages of Pacific herring and walleye pollock. As previously indicated, the bloom of *Neocalanus* may be prolonged during May when the surface layer is weakly stratified and cooler. At the present time, we are only beginning to understand how these conditions may affect predation on juvenile fishes. Lower temperatures will generally slow the growth of juvenile fishes. Yet, a prolonged *Neocalanus* bloom will probably accelerate juvenile growth if food is limiting and shelter juveniles from predation for a longer time. The converse may be true when the surface layer is more strongly stratified and warmer. Further study is needed to define the relationship among growth rates of juvenile fishes, the timing of the seasonal decline of the *Neocalanus* bloom, and mortality of juvenile fishes.

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Channel type and salmonid spawning distribution and abundance

David R. Montgomery, Eric M. Beamer, George R. Pess, and Thomas P. Quinn

Abstract: Consideration of fundamental channel processes, together with map-based and field investigations, indicates that stream channel type influences salmonid spawning distributions across entire channel networks and salmonid abundance within channel reaches. Our analysis suggests that salmonid spawning patterns in mountain drainage basins of the Pacific Northwest are adapted to, among other things, the timing and depth of channel bed mobility. We hypothesize that because the bed of pool–riffle and plane–bed reaches scours to a variable fraction of the thickness of alluvium, survival to emergence is favored by either burying eggs below the annual scour depth or avoiding egg burial during times of likely bed mobility. Conversely, annual mobility of all available spawning gravel in steeper step–pool and cascade channels favors either adaptations that avoid egg burial during times of likely bed mobility or selection of protected microhabitats. Consistent with these expectations, we find that salmonid spawning distributions track channel slope distributions in several west-slope Pacific Northwest watersheds, implying that spatial differences in channel processes influence community structure in these rainfall-dominated drainage basins. More detailed field surveys confirm that different channel types host differential use by spawning salmonids and reveal finer-scale influences of pool spacing on salmonid abundance.

Résumé : L'examen des processus fondamentaux des chenaux, combiné à des études cartographiques et à des travaux de terrain, montre que le type de chenal influe sur la distribution de la fraye des salmonidés à l'échelle du réseau de chenaux et sur l'abondance des salmonidés dans les tronçons des chenaux. Notre analyse permet de penser que les profils de fraye des salmonidés dans les bassins versants montagneux de la côte nord-ouest du Pacifique sont adaptés, entre autres, aux caractéristiques temporelles de la mobilité du lit des chenaux et à l'épaisseur de la couche concernée. Nous avançons l'hypothèse qu'étant donné que l'affouillement du lit des tronçons constitués de fosses et de rapides et des tronçons à lit plat touche une fraction variable de la couche d'alluvions, la survie jusqu'à l'émergence se trouve favorisée si les oeufs sont enfouis au-dessous du niveau d'affouillement ou si les femelles évitent d'enfouir leurs oeufs durant les périodes où le lit risque d'être affouillé. Par ailleurs, la mobilité annuelle de l'ensemble du gravier de fraye disponible dans les chenaux à pente prononcée constitués de seuils et de fosses et dans les cascades favorise soit les adaptations qui font que les femelles évitent d'enfouir leurs oeufs durant les périodes de mobilité probable du lit, soit le choix de microhabitats protégés. Conformément à ces observations, nous avons trouvé que les distributions de la fraye des salmonidés reflètent les distributions des chenaux selon leur pente dans plusieurs bassins du versant ouest de la côte nord-ouest du Pacifique, ce qui implique que les différences spatiales dans les processus des chenaux influent sur la structure des communautés dans ces bassins versants qui reçoivent d'importantes précipitations. Des études de terrain plus détaillées confirment que les différents types de chenaux suscitent des utilisations différentes par les salmonidés dans la période de reproduction et révèlent l'existence d'effets à plus petite échelle de l'espacement des fosses sur l'abondance des salmonidés.

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Introduction

Traditional explanations offered for controls on the timing and distribution of spawning among and within species invoke biological factors such as competition, egg size, prey availability, and body size (Chapman 1966; Gorman and Karr 1978; Moyle and Vondracek 1985; Beacham and Murray 1987) and physical influences such as intergravel flow, substrate size, and stream temperature (Stuart 1953; Schlosser 1985; Brannon 1987; Matthews 1987; Poff and Ward 1990). Although it is widely recognized that disturbance in general and discharge in particular affect stream fish communities (Horwitz 1978; Resh et al. 1988; Strange et al. 1992), the relationship between geomorphic processes and the phenology of reproduction and early life histories has received little attention.

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Salmonids occupy a variety of habitats within the stream network (e.g., Platts 1979; Li et al. 1987), and variation in the spatial and temporal distribution of spawning makes salmonids well suited for testing hypotheses related to the role of physical factors in determining life history traits. Anadromous salmon bury their eggs >20 cm below the channel bed (McNeil 1962; van den Berghe and Gross 1984; Chapman 1988), whereas smaller resident and anadromous trout have shallower egg burial depths, typically on the order of 5–10 cm (Needham 1961; Crisp and Carling 1989; Grost et al. 1991; Knapp and Vredenburg 1996). Larger females are capable of digging deeper redds (van den Berghe and Gross 1984; Crisp and Carling 1989), and egg survival to emergence is inversely related to the depth of scour during the period between spawning and emergence (Holtby and Healey 1986). Based on observations that chum salmon (*Oncorhynchus keta*) bury their eggs just below scour depths during bankfull flow, Montgomery et al. (1996*b*) suggested that egg burial depths represent an adaptation to depths of scour during typical winter storms.

Anadromous and resident species often inhabit different reaches of a channel network and spawn at different times. The usual explanation for spawning site selection is species-specific preferences for depth, velocity, and substrate (Burner 1951; Smith 1973). Spawning timing is typically attributed to synchronization of temperature-specific embryo development rates with seasonal patterns of prey availability for the progeny after they emerge (Beacham and Murray 1987; Brannon 1987). While such adaptations are important, we hypothesize that spawning distribution and timing also reflect the timing of bed mobility and the depth of scour in different portions of a channel network. In support of this hypothesis, we present evidence that fundamental spatial and temporal differences in channel processes influence salmonid spawning distributions and timing in rainfall-dominated drainage basins west of the Cascade crest in the Pacific Northwest (PNW). We further show that subreach-scale geomorphic characteristics also influence salmonid abundance and community composition. The strong association of reach-level channel types and salmonid distributions has important implications for salmonid conservation and watershed restoration efforts in the PNW.

Bed scour hypothesis for salmonid distributions

The hypothesis that bed scour depths constrain salmonid distributions is based on the premise that it is unlikely that a population could persist in an environment where annual scour depths consistently exceeded egg burial depths during the incubation period. In mountain drainage basins, interactions among channel morphology, bed roughness, and sediment transport lead to differences in patterns of scour between different types of channels (Montgomery and Buffington 1997). We hypothesize that such differences constrain the type of fish that could be adapted to different places in the channel network because of the relationship between fish size and egg burial depths. Below, we elaborate on this general hypothesis to lay out specific expectations for PNW channels.

Salmonids typically spawn in gravel- to cobble-sized substrate (e.g., Kondolf and Wolman 1993), and the depth of scour experienced by a redd will reflect differences in both the discharges to which it is exposed and geomorphic context. The frequency of flows associated with significant sediment transport varies for individual channels, but recurrence intervals for bankfull flow generally are on the order of 1–2 years (Williams 1978). Some bed mobility occurs at stages below bankfull (Jackson and Beschta 1982), but widespread bed mobility commonly occurs at a stage near bankfull (Carling 1983; Andrews 1984). Steep and low-gradient channels, however, fundamentally differ in the extent of bed mobility and the depth of scour during typical bed-mobilizing events.

Low-gradient reaches of mountain drainage basins generally exhibit gravel-bedded pool–riffle, forced pool – riffle, and plane–bed channel morphologies (Leopold et al. 1964; Church 1992; Montgomery and Buffington 1997). The bed of pool–riffle channels consists of the classic laterally oscillating sequence of bars, pools, and riffles. In contrast, plane–bed channels are characterized by a relatively featureless bed, and forced pool – riffle channels are those in which the majority of bars and pools are linked to local hydraulic convergence or divergence arising from local flow obstructions, such as large woody debris. Most of the bed-forming material within these channels may be suitable for spawning, and the full thickness of alluvium beneath the channel bed is rarely mobilized. Bankfull flows generally mobilize the streambed across the entire channel, and the average thickness of the layer in active transport, which sets the depth of scour, can be related to the rate of bedload transport (Carling 1987), although bedload transport and the associated scour depth can vary greatly across a channel during a single event (Hassan 1990). The bedload transport rate, in turn, is determined by the peak discharge's magnitude and duration (Milhous 1973; Jackson and Beschta 1982; Sidle 1988), which may vary dramatically from year to year, and the grain size of the bed-surface sediment, which may respond to changes in sediment supply (Dietrich et al. 1989). Increased sediment transport as a result of either higher discharges or greater sediment supply should increase the average depth of scour in low-gradient (i.e., pool–riffle and plane–bed) channels.

Steep alluvial channels tend to exhibit either step–pool or cascade morphologies. Step–pool reaches consist of large clasts organized into discrete channel-spanning accumulations that form a series of steps between pools containing finer material (Grant et al. 1990; Church 1992; Montgomery and Buffington 1997). In contrast, cascade channels are characterized by longitudinally and laterally disorganized accumulations of coarse bed material. Potential spawning gravel in step–pool or cascade channels typically occurs only locally in pools, the lee of large clasts, or other hydraulically sheltered locations. The stepped morphology and large grain sizes relative to the size of bedload material imply a high relative transport capacity (Montgomery and Buffington 1997). In contrast with lower-gradient channels, bedload transport in step–pool and cascade channels exhibits dual-threshold mobility, as large bed-forming clasts remain stable at discharges that mobilize gravel-sized material. Sediment transport rates in step–pool and cascade channels primarily reflect the availability of readily transportable sediment, and gravel-sized material is more frequently mo-

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Table 1. Hypothesized constraints on salmonids with different depths of egg burial relative to annual scour depths.

Spawning season	Egg burial depth (EB) versus scour depth (SC)	Rain-dominated low-gradient channels	Rain-dominated steep channels	Snow-dominated low-gradient channels	Snow-dominated steep channels
Spring	EB > SC	Possible	Possible	Possible	Precluded
Spring	EB < SC	Possible	Possible	Precluded	Precluded
Fall	EB > SC	Possible	Precluded	Possible	Possible
Fall	EB < SC	Precluded	Precluded	Possible	Possible

bile than coarser step-forming clasts (see review by Montgomery and Buffington 1997). During events that mobilize the between-step portions of the bed, active transport scours virtually the full depth of the gravel that could provide spawning habitat. Hence, there is a very high probability of mortality to buried eggs even during relatively common high flows.

We hypothesize that the fundamental difference in the mobility of potential spawning gravel in steep and low-gradient channel types described above constrains the potentially successful combinations of spawning timing and egg burial depths in mountain channel networks. In low-gradient channels where the active transport layer consists of a portion of the gravel thickness, two spawning strategies should be viable: (*i*) avoidance of egg burial in the gravel during the most likely time of bed mobility or (*ii*) burying eggs below the average annual scour depth. In contrast, avoidance of egg burial during times of likely bed mobility should be the only viable strategy in steep channels, where the active transport layer consists of the full thickness of potential spawning gravel.

In the PNW, the most probable time for annual high flows depends on whether runoff is rain dominated or snowmelt dominated. High flows in rain-dominated watersheds generally occur in winter, whereas high flows in snowmelt-dominated watersheds generally occur in spring. These differences lead to the expectation of spatial differences in the distribution of spring and fall spawning for salmonids in snowmelt-dominated and rainfall-dominated channels. A bed mobility control on spawning timing and egg burial depths predicts that in rain-dominated drainage basins, (*i*) fall spawning is not likely to be very successful (i.e., prevalent) in steep channels, (*ii*) fall spawning may be successful in lower-gradient channels if eggs are buried deeper than the average depth of scour, and (*iii*) spring spawning should be viable throughout the channel network.

Under the assumption that large fish can bury eggs beneath the annual scour depth and that small fish cannot, the constraints predicted by a bed mobility control on salmonid spawning can be summarized as follows for PNW channels (Table 1). Fall spawning in low-gradient channels should be viable only for large fish. In contrast, small salmonids could only spawn in spring, but could use both steep and low-gradient channels. The bed scour hypothesis further predicts that in snowmelt-dominated basins with annual high flows consistently in spring, the only fish that could spawn in low-gradient channels during spring would be large fish and that spring-spawning fish of any size would be severely disadvantaged in steep channels. Conversely, there would be no constraint on the distribution of fall-spawning fish; they could use the entire channel network. In contrast with basins with predictable annual high flows, basins in which annual high flows occur in either spring or fall (e.g., rain-on-snow dominated basins) would not be expected to have as significant a bed mobility influence on spawning distributions or timing.

Networkwide spawning distributions

In our multiscale investigation of geomorphic influences on salmonid spawning and abundance, we first examine the relationship between networkwide spawning distributions and channel types inferred from map-based analysis to provide an initial test of the hypothesized bed scour control on spawning distributions. Second, we analyze field surveys of spawner abundance in different channel types to investigate specific relationships between fish use and channel type. Finally, we analyze within-reach surveys to examine the degree to which subreach-scale variations in pool spacing influence salmonid abundance.

Our analysis of networkwide spawning distributions examines locations where data for spawning distributions were available from watersheds with a variety of channel types. This initial test of our hypothesis focuses on watersheds with rain-dominated hydrographs because (*i*) the potential for rain-on-snow events to produce high flow in many snowmelt-dominated basins would influence the predictability of the time of annual high flows and (*ii*) data available to us were from watersheds to the west of the crest of the Cascade Range.

Methods

Our test of predicted spawning distributions used data from the Clearwater River and portions of the Stillaguamish River basin in western Washington and from the Applegate River in southern Oregon. The 384-km^2 Clearwater River on the Olympic Peninsula, Washington, is ideal for testing our hypothesis because the basin had an extensive survey of spawning populations and fish distributions conducted in the early 1970's prior to intensive logging in the watershed (Edie 1975). Squire Creek is a 68-km^2 tributary that drains into the North Fork Stillaguamish River on the western slope of the Cascade Range in northern Washington. The basin consists of low-gradient channels that flow across the floodplain of the North Fork Stillaguamish River and steeper channels that emerge from bedrock-walled valleys. Squire Creek has no known barriers to fish migration, and spawner surveys have been conducted since 1974. The Applegate River watershed is an approximately 1970-km^2 drainage basin in the southern Oregon Coast Range, although its headwaters extend into northern California. The extent of the channel network used by different species of fish was summarized in a series of figures in the Applegate watershed assessment (Applegate River Watershed Council 1994).

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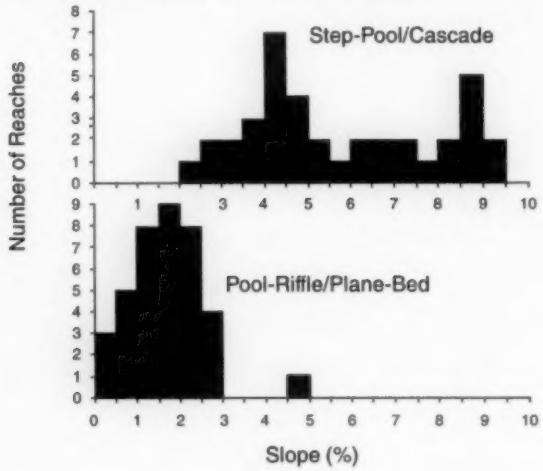
Fig. 1. Histograph of reach – average slopes for channels surveyed in field studies in western Washington State.



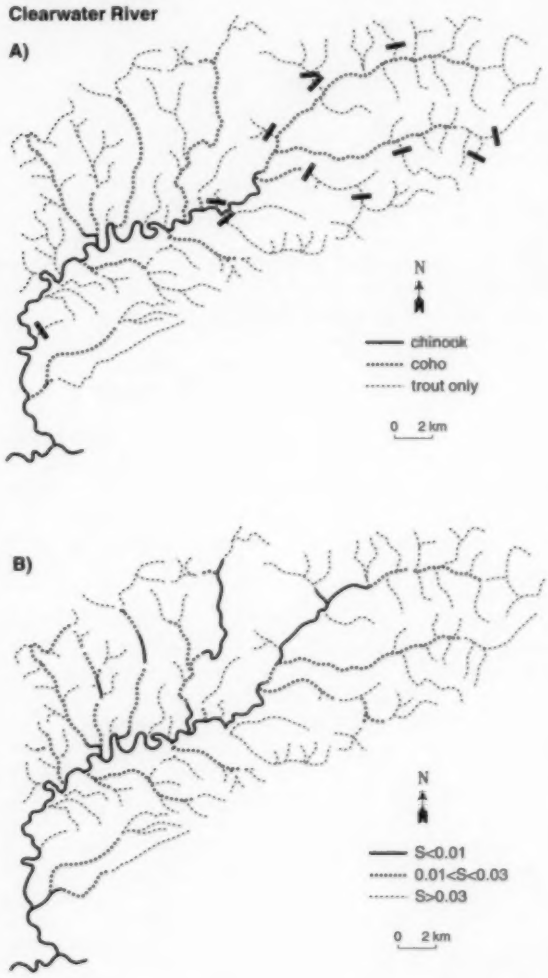
Together, these three basins allow a regionwide evaluation of predicted versus observed zones of fish use within mountain drainage basins.

In each of the watersheds for which maps of fish use were available, we measured channel gradients from U.S. Geological Survey 7.5′ topographic quadrangles. Channel gradients were determined by dividing the contour interval (typically 40′ or 12 m) by the distance between successive contours. Field measurements from previous studies of PNW channels indicate that pool–riffle and plane–bed reaches typically have gradients <3%, whereas step–pool and cascade reaches typically have gradients >3% (Fig. 1). Within the low-gradient channels, plane–bed and forced pool – riffle reaches typically occur on slope of 1–3%; channels with slopes ≤1% typically exhibit pool–riffle morphologies (Montgomery et al. 1995). Although most of the reaches that we have surveyed in various studies in the region conform to these general expectations, these slope categories are not absolute and channels with these morphologies do occur outside these typical slope ranges (Montgomery and Buffington 1997). Also, previous comparisons of channel slopes derived from field surveys and from 7.5′ topographic maps found that predicted gradients could be in error by as much as ±100%, in spite of an overall correspondence between map-derived and field-surveyed slopes (Montgomery et al. 1998). Channel gradients were used to classify the depicted channel networks into the general categories of low-gradient (<3%) and steep-gradient (>3%) reaches and to further subdivide the low-gradient channels in the Clearwater River and Squire Creek basins into <1 and 1–3% gradient reaches. We then compared the distribution of fish use with the gradient ranges predicted to be suitable for spawning by the bed scour hypothesis, as summarized in Table 1.

Results

Edie's (1975) map of fish distributions based on presence/absence surveys in the Clearwater River basin shows that large, fall-spawning chinook (*Oncorhynchus tshawytscha*) and coho salmon (*Oncorhynchus kisutch*) spawn in major

Fig. 2. Maps of the Clearwater River drainage basin on the Olympic Peninsula, Washington, showing (A) fish distribution zones defined by Edie (1975) (black bars across channels represent mapped fish passage barriers) and (B) channel gradients derived from U.S. Geological Survey 7.5′ topographic quadrangles. S, slope.



channels, whereas small, spring-spawning cutthroat trout (*Oncorhynchus clarki*) spawn in headwater channels. Large, spring-spawning steelhead trout (*Oncorhynchus mykiss*) occur throughout the network below migration barriers. The salmon and cutthroat trout distributions mirror the distribution of gradient ranges typical for different channel types (Fig. 2). Throughout the basin, the cutthroat-trout-only zone correlates with reaches with slopes >3%, the chinook zone correlates with reaches with slopes <1%, and the coho zone correlates with reaches with slopes of 1–3%. The general correspondence between fish distributions and channel slope supports our hypothesis for a fundamental geomorphic influence on salmonid spawning distributions because steep (i.e., >0.03) reaches in rain-dominated systems should not support fall-spawning salmonids (Table 1).

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Table 2. Percentage of total stream length identified in surveys within combinations of fish use zones and channel gradient.

	Channel gradient				% of fish distributed in predicted range
	<0.01	0.01–0.03	<0.03	>0.03	
Clearwater River					
Chinook zone	14	<1		0	100
Coho zone	6	17		1	95
Trout-only zone	<1	9		51	83
Stillaguamish River					
Chinook and coho zone			74	0	100
Trout-only zone			1	24	95
Applegate River watershed					
Chinook and coho zone			54	2	96
Trout only zone			2	42	95

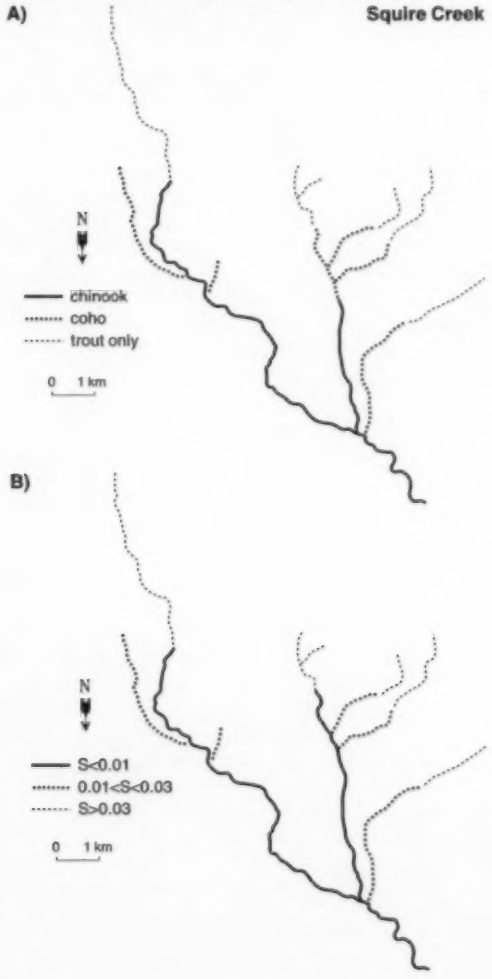

Fig. 3. Maps of the Squire Creek drainage basin in the northern Cascades, Washington, showing (A) fish distributions defined from field surveys and (B) channel gradients derived from U.S. Geological Survey 7.5′ topographic quadrangles.

A more quantitative examination of the correspondence of fish distributions and channel type further supports the predictions outlined in Table 1. Almost all of the 15% of the total channel length in the chinook zone is composed of channels with gradients <0.01 (Table 2). Similarly, the 52% of the total stream length composed of reaches with slopes >0.03 concides with the trout-only zone. In total, 100 and 95%, respectively, of the stream length in the chinook and coho zones occurred in the slope range typical for the channel types that the bed scour hypothesis predicts would be hospitable for large, fall-spawning species. Moreover, 83% of the mapped trout-only zone corresponds to the steeper channels, as also predicted by our hypothesis. Superimposed upon these basic patterns of species distributions are access limits imposed by debris jams and waterfalls or other migration barriers. These additional constraints improve the spatial correspondence between observed and predicted patterns of spawning.

In Squire Creek, chinook and coho use only the lower-gradient channels, and the trout-only zone occupies steeper channels (Fig. 3; Table 2). Spring-spawning cutthroat trout also use some lower-gradient channels, and steelhead spawn throughout the basin.

In the Applegate River, anadromous fish use the mainstem river and some of the primary tributary channels, whereas only trout use the smaller headwater channels (Fig. 4). Neglecting the reaches upstream of a dam that blocks anadromous fish from the basin headwaters, there is an excellent correspondence between fish use patterns and channel gradient (Table 2); over 95% of both of the fall-spawning anadromous and trout-only zones in this watershed consisted of channels in the gradient class predicted by our hypothesis. As in the Clearwater River, spring-spawning resident trout occur throughout the basin. Hence, in each of the three study basins, salmonid spawning distributions conform to the expectations of the bed scour hypothesis outlined in Table 1.

Reach-level channel type and fish abundance

Our analysis of field surveys of spawner abundance in different channel types focused on data collected in the Skagit and Stillaguamish rivers, in the northern Cascades, Washington. These surveys provided an additional quantitative field

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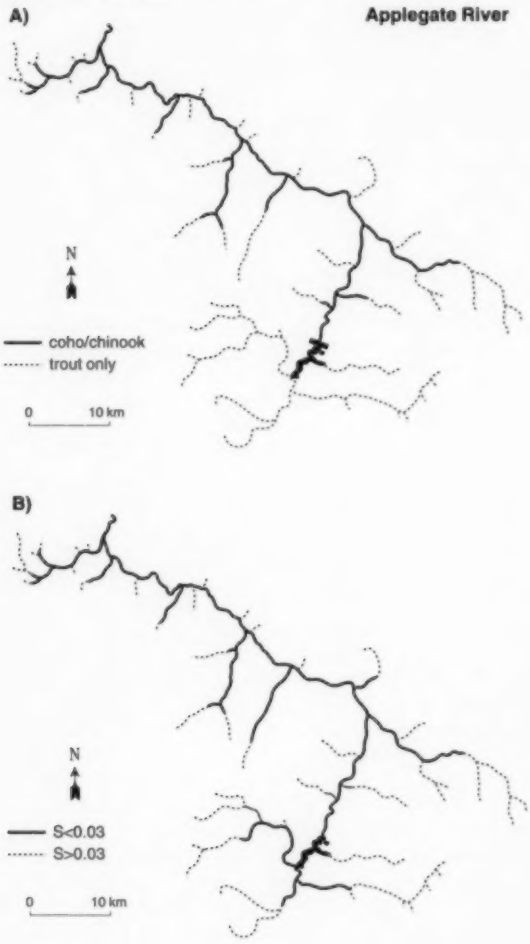

Fig. 4. Maps of the Applegate River drainage basin in the Oregon Coast Range showing (A) fish distributions reported in a watershed assessment (black bar across channel represents a dam that blocks anadromous fish passage) and (B) channel gradients derived from U.S. Geological Survey 7.5′ topographic quadrangles. S, slope.

test of the influence of channel type on spawning activity. In particular, these data allow closer examination of fish use patterns and abundance within the lower-gradient channels in the chinook and coho zones.

Methods

In the Stillaguamish River, we used data from repeated surveys of chinook redds and spawning coho conducted by the Washington Department of Fish and Wildlife over 2–23 years. We visited these reaches and classified each as pool–riffle, forced pool – riffle, plane–bed, or step–pool morphology following Montgomery and Buffington (1997). Mean and standard deviations for redds per kilometre and peak fish per kilometre were calculated for each reach. In the Skagit River, we used 50 reach-level surveys of chinook redds conducted in five tributaries to the Skagit River between 1991 and 1996, with several reaches being surveyed annually between 1994 and 1996. We also used 26 reach-level surveys of spawning coho. As for the Stillaguamish River, we visually classified the surveyed reaches into pool–riffle, forced pool – riffle, plane–bed, and step–pool morphology.

Our analysis of subreach-scale geomorphic influences on fish distribution and abundance focused on pool frequency data collected in the habitat surveys in the Skagit River. The spacing between pools is a fundamental channel attribute that varies widely in forest channels both between channel types and in response to the abundance of coarse woody debris that can force pool formation (Montgomery et al. 1995). Geomorphologists traditionally describe pool spacing in terms of the average length of channel between pools, expressed as the equivalent number of channel widths and termed channel widths per pool. For a given channel reach, a low pool spacing indicates many, closely spaced pools, whereas a high pool spacing indicates few, widely spaced pools.

Results

In records that extend over 2–23 years for the Stillaguamish River, the number of chinook salmon redds and spawning coho salmon per kilometre of channel varied with different channel types (Table 3). The density of chinook spawning varied dramatically by channel type, but similar types of channels exhibited similar redd densities. Redd densities within individual reaches were quite variable, but the mean values for pool–riffle channels ranged from 4.2 to 16.3 redds/km. These mean redd densities are very similar to the range of mean values of 2.5–13.8 redds/km for forced pool – riffle channels. In contrast, no spawning was recorded in plane–bed channels, although they occur in the same gradient range as the forced pool – riffle channels.

In the Stillaguamish River, the peak density of coho spawning also varied systematically by channel type (Table 3). Mean values ranged from 26.3 to 145.9 fish/km in pool–riffle channels and from 173.5 to 281.5 fish/km in forced pool – riffle channels. In contrast with chinook, plane–bed channels did support spawning coho, but at lower densities (8.0–37.9 fish/km). The consistent patterns of fish use over many years indicate channel-type-dependent differences in spawning use within the low-gradient channels usable by large fall-spawning fish in the Stillaguamish River; chinook and coho abundance was highest in forced pool – riffle channels and low in plane–bed channels.

Fish abundance data from the Skagit River revealed similarly strong relationships between channel type and fish use (Fig. 5A). Mean values of spawning density for pool–riffle and forced pool – riffle channels were 33.9 and 31.1 redds/km, respectively. The ranges in spawning use for pool–riffle and forced pool – riffle channels were also very similar. In contrast, the mean spawning density for plane–bed channels was only 2.0 fish/km. During the entire period of observation, only one chinook redd was observed in step–pool channels surveyed on the Skagit River, documenting the very low usage of these steeper channels predicted by our hypothesis, although the shortness of the reach resulted in an anomalously high value for redds per kilometre.

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Table 3. Data on channel type and number of observed salmonid redds for repeated spawner surveys along the North Fork Stillaguamish River, Washington.

	Years of data	Channel type and gradient	Reach length (cm)	Bankfull width (m)	Average redds/km	SD redds/km
Chinook salmon						
North Fork mainstem	2	PR 0.002	2700	70.0	16.3	3.3
North Fork mainstem	20	PR 0.003	6900	75.0	9.6	6.1
North Fork mainstem	20	PR 0.003	5600	60.0	12.0	7.6
Boulder River	16	PR 0.008	3950	20.0	4.2	3.6
Squire Creek	23	PR 0.005	1100	24.3	6.4	10.1
Furland Creek	2	FPR 0.015	800	10.0	13.8	1.4
Ashton Creek	2	FPR 0.010	800	10.0	8.8	3.5
Browns Creek	10	FPR 0.012	600	9.2	2.5	4.6
Brooks Creek	4	PB 0.010	1770	14.5	0.0	0.0
Rollins Creek	6	PB 0.027	532	20.0	0.0	0.0
Dicks Creek	4	PB 0.023	2414	17.0	0.0	0.0
Segelson Creek	2	PB 0.016	1931	12.7	0.0	0.0
Coho salmon						
North Fork mainstem	27	PR 0.003	6900	75.0	43.2	66.9
Boulder River	15	PR 0.008	3950	20.0	26.3	30.2
Squire Creek	20	PR 0.005	1100	24.3	145.9	143.0
Furland Creek	28	FPR 0.015	800	10.0	173.5	206.4
Ashton Creek	34	FPR 0.010	800	10.0	273.5	229.4
Browns Creek	36	FPR 0.012	600	9.2	281.5	210.1
Brooks Creek	3	PB 0.010	1770	14.5	37.9	44.5
Rollins Creek	7	PB 0.027	532	20.0	11.4	16.1
Dicks Creek	2	PB 0.023	2414	17.0	8.0	5.6
Segelson Creek	7	PB 0.016	1931	12.7	12.8	21.0

Note: PR, pool–riffle; FPR, forced pool – riffle; PB, plane–bed.

The difference in spawning use between channel types was even stronger for coho salmon in Skagit River tributaries (Fig. 5B). Mean values of spawning density in pool–riffle and forced pool – riffle channels were 110.9 and 101.0 redds/km, respectively, whereas the mean spawning density in plane–bed channels was 2.6 redds/km. No spawning coho were observed in step–pool reaches in the Skagit River tributaries. The consistent differences in these two watersheds revealed a strong association between spawning use and channel type.

Additional field surveys that used electroshocking and snorkeling techniques confirmed the presence of resident trout in the steeper channels that defined the "trout-only zone" in the Skagit and Stillaguamish watersheds. Several studies in the PNW have documented that native trout tend to remain close to their spawning areas (e.g., June 1981; Moore and Gregory 1988), implying that the distribution of juvenile fish closely reflects the species spawning distribution.

Spawning abundance of both chinook and coho in the Skagit River tributaries was inversely related to pool spacing (Fig. 6). Both pool–riffle and forced pool – riffle channels have pool spacings below the traditionally expected five to seven channel widths and have far greater redd abundance than the plane–bed channels. The pool spacing of more than five channel widths for plane–bed channels is consistent with other data for PNW channels (Montgomery et al. 1995). The uniformly low redd abundance (i.e., <20 redds/km) for both chinook and coho indicates lower salmonid abundance in plane–bed channels than in pool–riffle or forced pool – riffle channels. Moreover, the strong inverse relationship documents that both of these species have a distinct preference for spawning in reaches characterized by abundant pools.

Discussion

Our data and analyses reveal strong linkages between channel processes and fish use and abundance across a wide range of scales. The general correspondence of spawning distributions across mountain channel networks to those predicted by a simple hypothesis based on streambed scour implies a fundamental geomorphic forcing on broad patterns of salmonid distribution within PNW watersheds. At finer scales, specific habitat attributes appear to influence relative fish abundance and community composition within channel reaches. While we recognize that biological factors influence fish use and abundance across all of these scales, we nonetheless see a large role for channel processes at each scale.

The correlation of spawner abundance with channel type supports our overall hypothesis, but we do not discount stream temperature and microhabitat use (e.g., gravel size, depth, velocity) as important factors affecting the distribution and timing of salmonid spawning. Instead, genetic adaptations to temperature and behavioral responses to habitat may be superimposed on larger patterns controlled by bed mobility and discharge predictability. In some cases, stream temperature may adjust spawning timing by a matter of weeks, but bed mobility may dictate spawning season. In other cases, stream temperature may control spawning tim-

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Fig. 5. Percentile plots of redds per kilometre of stream length by channel type for (A) chinook and (B) coho salmon in tributaries of the Skagit River, Washington. Solid lines within boxes are median values, broken lines are inner and outer quartiles, tops and bottoms of boxes are the 10th and 90th percentiles, and *n* values are the number of sample reaches in each distribution. PR, pool–riffle; FPR, forced pool – riffle; PB, plane–bed; SP, step–pool.

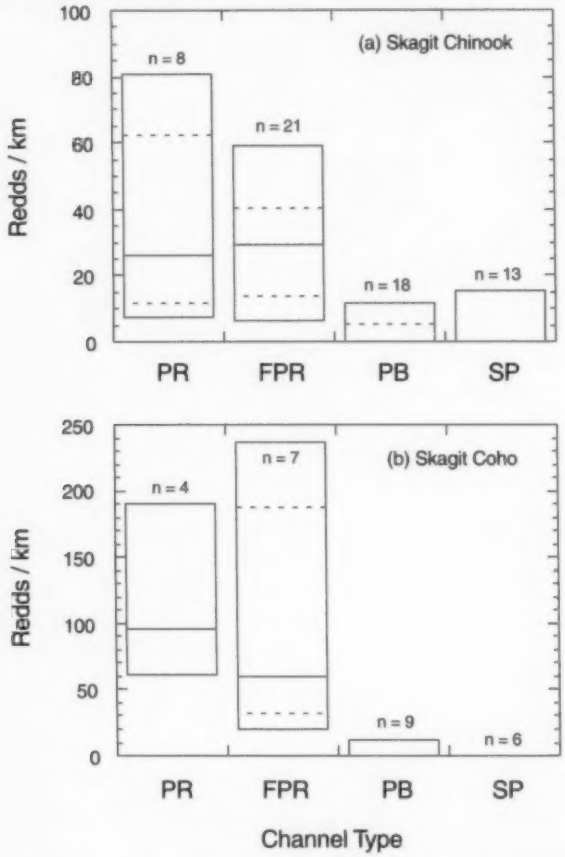
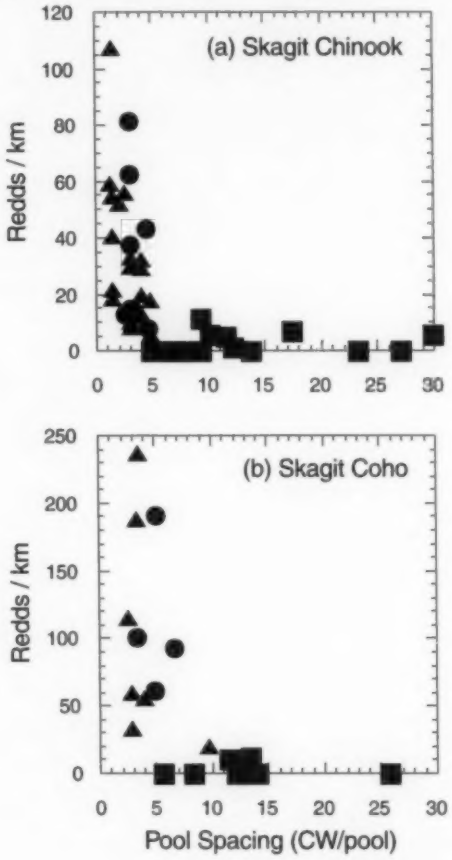


Fig. 6. Redds per kilometre of stream length versus pool spacing (average length of channel between pools in units of channel width (CW) per pool) for (A) chinook and (B) coho salmon in tributaries of the Skagit River, Washington. Squares represent plane–bed reaches, triangles represent forced pool – riffle channels, and circles represent pool–riffle channels.



ing, and annual differences in bed scour may simply influence the abundance of different age classes. In other words, the influence of temperature, flow conditions, and streambed scour may be more or less important in different circumstances.

We would expect that spawning success may have a greater stochastic component where the seasonal timing of high flows has substantial variability. Consequently, we expect bed mobility to be most relevant in environments with predictable hydrologic regimes and spatially variable channel types. Such conditions are likely to characterize mountain drainage basins in humid-temperate environments; the proposed bed scour mechanism may be less important in areas with uniform channel types or unpredictable hydrologic regimes. Furthermore, we would expect the temperature regime to be more important in mountain drainage basins with more extreme ranges in temperature than our study basins, such as in basins in the continental interior.

We are aware of apparent exceptions to our hypothesis that upon closer inspection reflect the influence of other important processes or controls. Microhabitat selection, for example, may influence spawning success through use of hydraulically sheltered locations with relatively stable gravel (e.g., Knapp and Vredenburg 1996). Similarly, sediment impounded behind log jams may decrease local channel gradients enough to alter channel type, and hence fish use, over long stretches of stream channel (Montgomery et al. 1996*a*). In addition, fine-scale stretches of low-gradient channel types (such as forced pool – riffle reaches) can occur within generally steep headwater valleys, and these areas may provide local habitats. Spawning in such localized areas may allow species to successfully occupy portions of a channel network that would otherwise be inhospitable. Conversely, elimination of favorable microhabitat may decimate local populations that rely on such areas in steep mountain streams. The prevalence of side channel spawning along some channel reaches also provides the potential for apparent exceptions to our hypothesis, as side channels should not

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scour to depths comparable with the main channel and can thereby present safe spawning environments for small fish. Such factors may be more or less important in particular stream systems. Hence, not every apparent exception falsifies the basic hypothesis regarding scour depths and spawning distributions, which is best viewed as one of many conceptual frameworks within which to test and explore large-scale controls on spawning distribution and timing.

Several workers report that the occurrence of bed-mobilizing events in both fall and spring facilitates the coexistence of spring- and fall-spawning trout in steep Sierran channels (e.g., Seegrest and Gard 1972; Kondolf et al. 1991). Moreover, both spring- and fall-spawning species of trout are present in some steep channels of the Cascade Range that experience both large winter rainstorms and significant springtime snowmelt. The presence of both spring- and fall-spawning trout in these steep channels suggests that unpredictable disturbance timing may prevent exclusion of either spawning population. Despite general consistency between these examples and our hypothesis, further tests and experimentation are needed to refine the regional relevance of our hypothesis, the influence of local hydraulically sheltered environments on exceptions, and the geography of its importance relative to other factors that influence the reproductive success of salmonids.

Implications for conservation

Correlation of fish abundance and channel type could allow for more direct linkages between assessment of channel morphology, habitat quality, and species use and abundance. Chinook and coho abundances are high in pool–riffle and forced pool – riffle channels and are low in plane–bed and step–pool channels. Also, the inverse correlations between anadromous fish abundance and pool spacing imply that dramatic changes in salmonid abundance would follow changes in pool frequency or channel type. As forced pool – riffle and plane–bed channels can both occur within the 1–3% gradient class (Montgomery et al. 1995), this implies that loss of wood debris from a forced pool – riffle channel, and that results in its conversion into a plane–bed morphology (Montgomery and Buffington 1997), will be accompanied by a local decrease in salmon abundance. Addition of simple morphological distinctions appears to hold great potential for increasing the relevance and utility of much of the stream habitat information collected in the mountainous PNW. Considered broadly, the association of channel type and salmonid distributions and abundance provides a framework within which to investigate and interpret population response to changes in sediment supply, discharge regime, or large woody debris.

Our interpretations also imply that changes in scour depths in low-gradient channels should preferentially impact certain species of salmonids. Fall-spawning populations (e.g., chum and coho) in coastal rain-dominated channel systems should be very sensitive to changes in bed scour depths, whereas spring-spawning populations (e.g., cutthroat trout) in these systems should be less sensitive to enhanced scour from increased sediment supply. Considered in this context, the recent dramatic reduction in mean body size of many salmon populations (Bigler et al. 1996) is cause for concern. Not only would smaller females have lower fecundity (Beacham and Murray 1993), but they would also dig shallower, more scour-prone redds.

Conclusions

Salmonid spawning distributions and reproductive success reflect a complicated interplay of biological and physical processes, and our findings emphasize the multiscale influence of geomorphic processes on salmonid abundance. At the scale of entire river networks, differences in bed mobility appear to influence salmonid distributions and spawning timing. Channel types defined by bed morphology appear to explain broad patterns of anadromous and resident species distributions and correlate with spawning densities of different species. Variations in within-reach habitat characteristics also affect the relative abundance of anadromous salmonids. Although our results imply that fundamental physical constraints help set patterns of salmonid use throughout mountain drainage basins, the relative importance of the effects of physical and biological factors on salmonid distribution and spawning timing is likely to vary both locally and regionally. Although other processes may dominate spawning timing in systems with temperature ranges beyond a species' tolerance (or, for example, in spring-fed channels with a uniform flow regime and infrequent bed mobility), we conclude that there is strong, multiscale influence of geomorphological processes on salmonid distribution and abundance in PNW channels.

Acknowledgements

We thank John Buffington and N. Phil Peterson for insightful discussions, Tamara Massong for undertaking the tedious job of measuring channel slopes throughout the Clearwater River basin, Bob Pfeiffer, Mark Teske, John Hisata, and Mark Schuck for information on spawning timing in steep mountain channels, Washington Department of Fish and Wildlife staff for conducting some of the redd surveys, and Bill Platts, Mark Schuck, D.W. Chapman, and anonymous reviewers for critical comments on draft manuscripts. This work was supported in part by the Sediment, Hydrology, and Mass Wasting Committee of the Washington State Timber/Fish/Wildlife agreement. T.P.Q. also acknowledges support of the H. Mason Keeler endowment.

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Slow growth and decomposition of mosses in Arctic lakes

Kaj Sand-Jensen, Tenna Riis, Stiig Markager, and Warwick F. Vincent

Abstract: Aquatic mosses are often the exclusive form of macrophytic vegetation in Arctic lakes. Despite the cold nutrient-poor water and the short ice-free summer, the mosses form dense stands on the lake bottom down to great depths. The environmental conditions suggest that moss growth and decomposition are extremely slow, but logistical and methodological difficulties have so far precluded direct measurements of the processes. Here, we use temporal changes in the size and density of leaves along the axis of moss shoots collected from different depths in Char Lake and North Lake in the Canadian High Arctic to reconstruct the annual growth and decomposition of the mosses during the past 10–17 years. Our results show low but remarkably constant annual elongation rates (about 10 mm·shoot^{-1}) in the long-lived shoots that carry green leaves for several years and decompose slowly. Cold temperatures and low nutrient supply in combination with the short Arctic growing season can account for the low growth rate, the low decomposition rates, and the unprecedented longevity of these moss communities relative to other submerged macrophytes.

Résumé : Les mousses aquatiques sont souvent la seule forme de macrophytes dans les lacs de l'Arctique. Malgré que les eaux soient froides et pauvres en nutriants et que les lacs soient déglacés durant seulement une courte période dans l'Arctique, les mousses forment des peuplements denses sur le fond des lacs jusqu'à de grandes profondeurs. Les conditions environnementales dans cette région laissent penser que la croissance et la décomposition des mousses y sont extrêmement lentes, mais des difficultés logistiques et méthodologiques ont à ce jour empêché la mesure directe de ces processus. Nous avons utilisé les changements temporels dans la taille et la densité des feuilles le long de la tige des pousses de mousses recueillies à différentes profondeurs dans les lacs Char et North, dans le Grand Nord canadien, pour reconstruire la croissance et la décomposition annuelles des mousses au cours des 10 à 17 dernières années. Nos résultats montrent que les taux d'élongation annuels sont bas mais remarquablement constants (environ 10 mm·pousse^{-1}) chez les pousses longévives qui portent des feuilles vertes durant plusieurs années et se décomposent lentement. Les basses températures et la faible quantité de nutriants, de pair avec la courte saison de croissance dans l'Arctique, peuvent expliquer le faible taux de croissance, les faibles taux de décomposition, et la longévité de ces communautés de mousses, qui dépasse celle des autres macrophytes submergés.

[Traduit par la Rédaction]

Introduction

Mosses are common in unproductive terrestrial and aquatic habitats and are mainly regarded as stress-selected, slow-growing organisms (Furness and Grime 1982). In temperate regions, aquatic mosses dominate the vegetation in nutrient-poor, acid lakes (Grahn 1977; Toivonen and Huttunen 1995), and in transparent alkaline lakes, they grow at very low irradiance and temperature at depths below the rooted vegetation (McIntire et al. 1994; Middelboe and Markager 1997). In Arctic and Antarctic lakes, mosses are typically the only macrophytes present (Bodin and Nauwerck 1968; Welch and Kalff 1974; Priddle 1980).

Aquatic mosses can extend to great water depths and can apparently survive at only 0.1–2% of the surface irradiance (Frantz and Cordone 1967; McIntire et al. 1994). The deep-growing mosses have been suggested, based on short-term measurements of photosynthesis and respiration, to grow extremely slowly and live for many years (Bodin and Nauwerck 1968). These suggestions have not been confirmed due to the lack of direct measurements of growth and longevity of mosses in the natural environment. Short-term measurements of photosynthesis and respiration during summer cannot provide reliable data for evaluating the annual growth and longevity in Arctic lakes, which are covered by ice for more than 10 months a year (Schindler et al. 1974). Field incubation techniques are also difficult to apply because the mosses grow in a dense quilt of live and dead shoots that is disturbed by experimental manipulation. Moreover, the Arctic lakes are difficult to study because of the adverse climate and the remote location. Measurement of the long-term growth and decomposition of aquatic mosses would, however, be rewarding because this could help deter-

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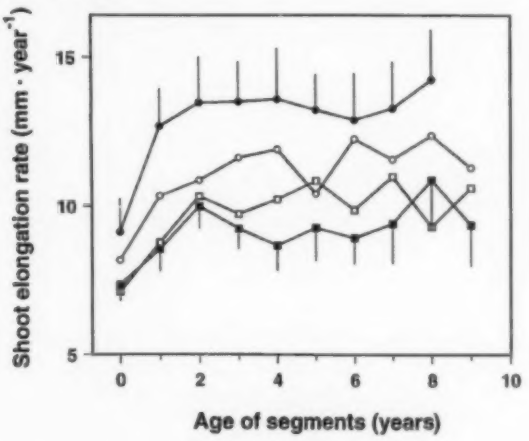
Fig. 1. Annual shoot elongation of *Drepanocladus revolvens* at depth in Char Lake. Mean elongation rate was reconstructed for every annual segment 8–10 years back in time based on measurements on 26–48 shoots from each depth. The 95% CL is only shown one-sided for the highest and the lowest values to ensure clarity. The 95% CL averaged 12% of the mean annual growth rate. ●, 3.8 m depth; ○, 6.8 m depth; ■, 10.8 m depth; □, 13.5 m depth.



mine their role in carbon and nutrient cycling in the Arctic lakes and in the many acidified lakes at lower altitudes where mosses have become more abundant (Grahn 1977; Roelofs 1983).

Here, we reconstruct the growth and life span of *Drepanocladus revolvens* var. *intermedius* (Schimp.) Anderson et al. and *Calliergon giganteum* Schimp. at depth in Char Lake and neighbouring North Lake, High Arctic Canada (74°42′N, 94°50′W), based on seasonal changes in morphology using methods analogous to those recently developed for mosses in a temperate lake (Riis and Sand-Jensen 1997) and previously applied to terrestrial plants and seagrasses (Callaghan et al. 1978; Duarte et al. 1994). The reconstruction technique has the advantage that a large representative sample of moss shoots can be collected from different sites and depths on a single occasion to determine growth and demographic variables.

Study sites and methods

The two Arctic lakes are located in a polar region with low annual precipitation (average 136 mm·year^{-1}, McCann et al. 1972) and relatively high annual irradiance (average 6240 mol photons·m^{-2}·year^{-1}, 400–700 nm, Schindler et al. 1974). Lakes in the region are alkaline, poor in nitrogen and phosphorus, and have low phytoplankton biomasses and transparent water (Schindler et al. 1974). Char Lake (53 ha, 28 m deep) was intensely studied over several years in the 1970's, and the temperature, light climate, and water chemistry of the lake are the best known for any High Arctic lake (Schindler et al. 1974). During collection of mosses in August 1995, we determined water temperature and the spectrally averaged light attenuation coefficient (K_d, per metre) for photosynthetically active radiation (400–700 nm at 10-nm intervals) recorded with a LiCor 1800 spectroradiometer at depths of 2–20 m in Char Lake and 1–6 m in North Lake. We also determined the chlorophyll concentration at 0.5 m depth on triplicate filtered water samples followed by fluorometric measurements according to the method of Strickland and Parsons (1972). The chlorophyll concentration was 0.46 μg·L^{-1} and K_d was 0.14·m^{-1} in Char Lake. The K_d closely resembled the values encountered in the earlier studies. Therefore, we used continuous measurements of surface irradiance for the last 10 years at a metereological station located close to Char Lake but the earlier comprehensive 3 years of measurements of light attenuation through snow, ice, and water (Schindler et al. 1974) to estimate the mean annual irradiance reaching moss populations at depth in the lake. Likewise, we used the 3 years of measurements of water temperature at depth to determine the mean degree-days integrated over the year at the different water depths.

North Lake (70 ha, 12 m deep) is more shallow, has higher phytoplankton concentration (0.90 μg chlorophyll a·L^{-1}), and is less transparent (K_d = 0.29·m^{-1}) than Char Lake. To obtain a crude estimate of the irradiance reaching the mosses at depth in North Lake, the light attenuation through ice and snow was assumed to be the same as for Char Lake. Char Lake is covered by ice and thin snow for most of the year, apart from a brief summer period (<8 weeks) between July and September, and mean annual water temperatures are close to 1°C (Schindler et al. 1974). Mean annual water temperature in North Lake likely resembles that in Char Lake, but maximum water temperatures in August 1995 were higher in the shallower North Lake (6°C) than in the deeper Char Lake (4°C).

Moss shoots were collected with a rake from several water depths in the two lakes. From each depth, between 10 and 50 live shoots were pressed and dried between water-absorbent paper for later investigations in the laboratory. The shoots had distinct annual segments presumably because leaves were larger and were produced more frequently in summer than during the rest of the year. Such annual growth segments are common among many temperate and Arctic plants as a result of periodicity in irradiance and temperature (Callaghan et al. 1978; Havström et al. 1995; Riis and Sand-Jensen 1997). Likewise, we regard the periodic growth segments of the mosses as annual segments due to the extreme annual periodicity of light availability in the Artic lakes. This kind of perodicity in environmental variables other than irradiance and temperature is not known. The distinct seasonal pattern of the Arctic mosses permitted us to determine the length, the dry mass, and the content of carbon, nitrogen, and phosphorus of every annual segment for 8–10 years back in time for most shoots and up to 17 years for particularly long shoots. Measurements of carbon and nitrogen were made on a Carbo-Erla CHN analyzer. Phosphorus was determined by means of oxidation with peroxidisulphate (Koroleff 1976).

Results

Both species of mosses grew at low rates in Char Lake and North Lake. The two recent annual growth segments in shoots of *D. revolvens* from Char Lake were shorter than the older segments, and they had not finished elongation (Fig. 1). The leaves remained green for at least 4 years, and the length of annual segments was remarkably constant between 2 and 9 years. The mean elongation rate of the fully grown annual segments of *D. revolvens* declined slightly but significantly at depth in Char Lake from 13.2 mm·shoot^{-1}·year^{-1} at 3.8 m depth to 10.3 mm·shoot^{-1}·year^{-1} at 13.5 m depth (Table 1). Shoots of *C. giganteum* elongated at a similar rate as *D. revolvens* at 10.8 m depth in Char Lake. Low annual mean shoot elongation was also observed for *C. giganteum* in North Lake between 17.9 mm·shoot^{-1}·year^{-1} at 4.5 m depth and 11.4 mm·shoot^{-1}·year^{-1} at 6.5 m depth (Table 1). Annual segments of *C. giganteum* reached their fi-

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Table 1. Annual irradiance, degree-days, and shoot demography of two moss species at depth in Char Lake and North Lake in the Canadian High Arctic.

Lake and species	Depth (m)	Irradiance (mol photons·m^{-2}·year^{-1})	Degree-days	Elongation rate (mm·shoot^{-1}·year^{-1})	Growth rate (mg dry weight·shoot^{-1}·year^{-1})	Longevity (years)	Decomposition rate (year^{-1})
Char Lake							
D. revolvens	3.8	1245	260	13.2±0.6*d*	2.8±0.3*d*	9.4±0.8*cd*	–0.13±0.05*ab*
	6.8	820	290	11.5±0.6*c*	2.0±0.2*b*	8.8±0.7*bc*	–0.11±0.06*a*
	10.8	485	305	9.3±0.4*a*	2.3±0.2*bc*	9.1±0.8*cd*	–0.11±0.06*a*
	13.5	340	325	10.3±0.5*b*	1.3±0.1*a*	10.1±1.3*d*	
C. giganteum	10.8	485	305	9.9±0.8*ab*	2.6±0.3*cd*	8.8±2.0*abcd*	–0.11±0.08*a*
North Lake							
C. giganteum	4.5	780	—	17.9±1.4*e*	2.7±1.3*cd*	7.0±1.5*a*	–0.18±0.12*ab*
	5.5	670	—	13.6±0.8*d*	1.0±0.1*a*	8.1±1.2*abc*	–0.32±0.14*b*
	6.5	580	—	11.4±0.6*c*	1.2±0.2*a*	7.5±1.6*ab*	–0.32±0.30*b*

Note: Mean elongation rate and growth rate based on weight are given as the annual rates for fully grown shoots. Longevity represents the mean age of shoots still with distinct annual segments formed by the dead leaves. Decomposition rate was calculated from an exponential fit to the decline of dry mass of annual segments older than 4–6 years in *Drepanocladus revolvens* and 3–4 years in *Calliergon giganteum*. The ±95% CL is given for 26–48 shoots for *D. revolvens* and 9–28 shoots for *C. giganteum*. Values followed by different letters are significantly different among rows within columns ($P < 0.05$, ANOVA).

nal length already after the first year, and similar to *D. revolvens*, there was little interannual variability in shoot length.

The dry mass of the annual segments changed markedly with age along the shoot axis of *D. revolvens* (Fig. 2). The annual segments reached the maximum dry mass in the second to third year at 3.8 m depth, while they reached the maximum weight later at greater depth. The dry mass of fully grown annual segments was markedly higher in shallow water than in deep water (Fig. 2) because the size and density of leaves along the shoot axis were higher in the shallow-water than in the deep-water populations. Beyond the age of maximum dry mass, the annual segments gradually lost weight (Fig. 2) along with a visual change of the leaves from fresh green to pale green, then to brown, and finally to black, showing an ongoing senescence. Senescence was postponed to gradually older segments of the shoots at increasing depth. In populations of *D. revolvens* between 3.8 and 10.8 m depth with sufficient annual generations included in the material, the dry mass of annual segments declined exponentially from the age of maximum dry mass to the age of 10–15 years at a rate of 0.11–0.13·year^{-1} (half-life about 6 years), while no mass decline was apparent at 13.5 m (Fig. 2; Table 1). The mass decline is primarily due to loss of leaf material, while the stem is more resistant.

The annual growth rate in dry mass of *C. giganteum* at 10.8 m in Char Lake was not significantly different from the annual growth rate of *D. revolvens* at the same depth (Table 1). Likewise, the dead annual segments of *C. giganteum* in Char Lake lost mass at the same rate as in *D. revolvens*. Similar growth rates of *C. giganteum* in North Lake were observed at 4.5 m, while rates were twofold lower at 5.5 and 6.5 m (Table 1). The rate of mass loss in old segments of *C. giganteum* in North Lake was markedly higher (0.18–0.32·year^{-1}, Table 1) than in Char Lake.

The moss tissue was poor in nitrogen and phosphorus at all ages and depths, but the contents of carbon, nitrogen, and phosphorus were higher in the youngest apical segments than in older parts (Table 2). The nitrogen content was particularly low in mosses from Char Lake, showing C:N mass ratios of 32–46, while ratios were 17–24 in mosses from North Lake (Table 2). The nitrogen concentrations in Char Lake mosses are among the lowest reported for submerged macrophytes and markedly lower than the critical concentrations proposed for nitrogen-limited growth (Duarte 1992). Phosphorus concentrations in the mosses were also low, although the C:P ratios (164–410) were within the range of critical phosphorus concentrations proposed for macrophyte growth (Duarte 1992). The low N:P ratios, particularly in mosses from Char Lake (6.4–9.4), also suggest that nitrogen rather than phosphorus may limit the rates of moss growth and decomposition.

Discussion

The reconstruction technique allowed determination of the annual mean shoot elongation about 9 years back in time with a high reproducibility at every depth (i.e., 95% CL of mean annual elongation rate was 12% for *D. revolvens* and 22% for *C. giganteum*). The mosses grew slowly in length and at slightly lower rates at increasing depth, while the mean values did not change significantly among years at any depth (Fig. 1). This result suggests that differences in growth conditions among years were small or, alternatively, that mosses allocated resources between annual segments of different ages maintaining a relatively constant elongation rate every year independent of the suitability of growth conditions in any particular year. The extensive variation in dry mass of annual segments at depth shows that the suitability of growth conditions is indeed variable, but the mosses can maintain about the same annual elongation by varying the size and density of the leaves (Table 1; Fig. 2).

We found no relationship between the annual surface irradiance and the growth rate of the mosses, but the interannual changes in light availability for the mosses in the lakes are also much more dependent on the variable light attenuation through snow, ice, and water than on the incident irradiance, and these attenuation components are not measured routinely. The perennial nature of the moss shoots presumably has the advantage that storage and allocation of resources

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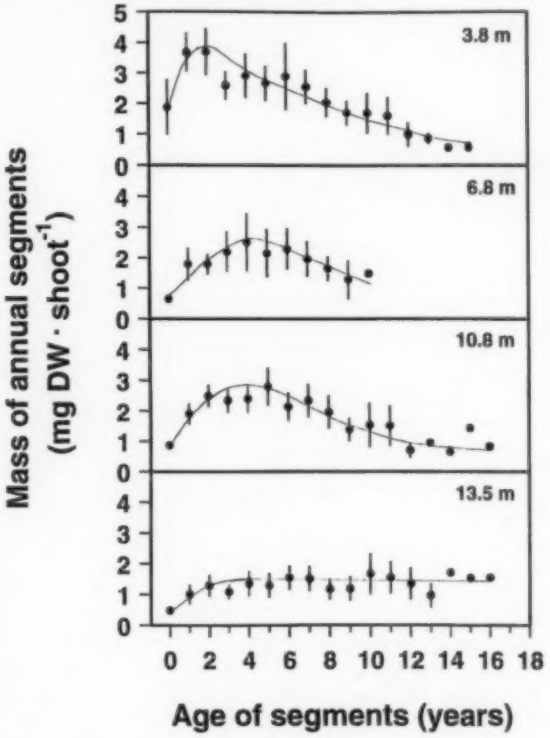
Fig. 2. Mean dry mass (± 95% CL) of annual segments up to 17 years old in 26–48 shoots of *Drepanocladus revolvens* from each of the different depths in Char Lake. The curve for dry mass versus shoot age was fitted by eye in the young segments, while the exponential rate of decline of dry mass in old segments at depths of 3.8–10.8 m was fitted by log-linear regression. The oldest annual segments have no error bars because fewer than five segments were available.



are possible such that new green tissue can be produced after the long arctic winter, and perhaps after even longer dark periods, if ice and snow cover fails to disappear every summer. Functionally, the aquatic mosses may resemble the lignified arctic heather *Cassiope tetragona* (L.) D. Don., which maintains photosynthetic leaves for about 4 years and continues to produce new shoot segments during cold arctic summers with late snow melting, although the number and size of the leaves are smaller than during more suitable warm summers (Havström et al. 1995).

The annual mean elongation of the moss shoots is low for both Arctic species, while the mean age of the shoots, still with discernible annual growth segments, is high (i.e., 7.0–10.1 years, Table 1). The low growth rates and high longevity of the Arctic mosses are unprecedented among all previous studies on freshwater rooted macrophytes (reviewed by Nielsen and Sand-Jensen 1991). The only previous measurements of aquatic moss growth and longevity are for populations of *Sphagnum subsecundum* coll. and *Drepanocladus exannulatus* (Gümbel) Warnstorf from the mesotrophic Grane Langsø in Denmark (Riis and Sand-Jensen 1997). Here, the annual shoot elongation in the thermocline and upper hypolimnion at 6–10 m depth was about 20-fold higher (226–248 mm·shoot^{-1}·year^{-1}) and mean shoot longevity only 0.95–1.35 years. The most likely explanation for the low growth rate and the high longevity of the mosses in the Arctic lakes is the cold water, the short summer period of adequate light for net photosynthesis, and the nutrient-poor tissue. The annual irradiances received by the moss populations were low but not systematically different between the temperate Grane Langsø (144–621 mol photons·m^{-2}·year^{-1}, 400–700 nm, Riis and Sand-Jensen 1997) and the two Arctic lakes (342–1245 mol photons·m^{-2}·year^{-1}, Table 1). However, light availability is much less evenly distributed over the year in the Arctic lakes. The annually cumulative degree-days were 2069–2964 at 6–10 m depth in the temperate lake and only 261–327 in the Arctic lakes. Moreover, the nitrogen content was much higher (3.1–3.7% dry weight) in *Sphagnum* mosses from the temperate lake, with C:N ratios of 11.2–13.6; these are threefold lower than the ratios found in the mosses from Char Lake (Riis and Sand-Jensen 1997) (Table 2).

Low nutrients and cold temperatures may constrain photosynthesis and growth of the mosses in these Arctic lakes. Nutrient shortage limits capital investment in enzymes and new growth products, while low temperature limits the specific catalytic capacity per enzyme available and, thereby, the possible gain from the investment of a certain amount of nutrients. These constraints on enzymatic capacity should be particularly strong in Arctic lakes in which light is received as a single, almost continuous dose during a short 2- to 3-month period. Marine macroalgae in Arctic regions can, in contrast, obtain a higher productivity and tissue turnover because high nutrient availability in part can compensate for the low temperatures by investment in greater enzyme concentrations (Davison et al. 1991; Markager and Sand-Jensen 1994). This compensation is precluded in nutrient-poor Arctic lakes.

Cold temperatures and low nutrient concentrations can also account for the longevity of the Arctic mosses and the slow weight loss of dead tissue. Thus, rates of growth, senescence, and decomposition should be closely coupled and regulated by the same intrinsic and extrinsic factors (Enriquez et al. 1993; Cebrian and Duarte 1995). The annual rate of weight loss of dead moss tissue from Char Lake was only about 0.11–0.13·year^{-1} or 20- to 200-fold lower than the values for other freshwater macrophytes mostly obtained in experiments in temperate regions at higher temperatures (reviewed by Enriquez et al. 1993). The rates of weight loss of detritus derived from temperate reed plants are also about 10-fold faster than the rates for the Arctic mosses at similar concentrations of tissue nitrogen (Enriquez et al. 1993).

Despite the low growth rates, the Arctic mosses are capable of forming dense stands due to the slow loss rates and the longevity of the tissue (Welch and Kalff 1974). They can also contribute significantly to the pool of organic detritus because rates of microbial degradation are expected to be strongly limited by low temperature, low nutrient concentration, and low activity of invertebrate detritivores, which accelerate degradation in warmer aquatic habitats (Webster and Benfield 1986).

The reconstruction technique presented here is straightforward and allows an inexpensive and precise analysis of growth, life span, and decomposition of moss populations

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Table 2. Carbon content and elemental mass ratios in young and old annual segments of *Drepanocladus revolvens* and *Calliergon giganteum* at depth in Char Lake and North Lake, Canadian High Arctic.

		Carbon (% dry weight)		C:N ratio		C:P ratio		N:P ratio	
Lake and species	Depth (m)	Young	Old	Young	Old	Young	Old	Young	Old
Char Lake									
D. revolvens	3.8	30.6	26.9±0.7*bc*	43	46±2*d*	332	410±17*c*	7.7	8.9±0.3*a*
	13.5	39.9	29.7±0.8*c*	32	33±1*c*	206	302±38*ab*	6.4	9.4±1.9*ac*
C. giganteum	10.8	37.9	27.4±2.8*bc*	33	33±3*c*	266	368±47*bc*	8.1	9.2±4.2*abc*
North Lake									
C. giganteum	4.5	25.4	22.2±1.8*a*	20	20±1*a*	366	333±62*abc*	8.6	15.9±1.9*d*
	5.5	29.7	29.4±2.7*c*	18	23±1*b*	386	313±90*ab*	21.1	12.6±5.7*cd*
	6.5	26.4	26.0±3.5*b*	17	24±1*b*	164	281±76*a*	9.4	12.1±3.6*bc*

Note: Young annual segments representing the recent 1.5-year segments were pooled for all individuals of each species and depth. Old annual segments (>2 years) were pooled for each year and an overall mean was calculated for all years. Mean values (±95% CL) represent 26–48 shoots for *D. revolvens* and 9–28 shoots for *C. giganteum*. Values followed by different letters designate significantly different values among rows within columns ($P < 0.05$, ANOVA).

from remote regions with adverse climate and sites difficult to access. The formation of a dense quilt of live and dead moss shoots on the lake bottom and the slow rates of growth and decomposition of the Arctic mosses preclude traditional incubation methods, while the reconstruction technique benefits from the slow rates of the processes, allowing several years of growth and decomposition to be represented in just one collection of the moss shoots. In future use, however, independent tests are recommended to acertain that growth segments are indeed annual, although no other explanation appears likely today. With methodological improvements the broad-scale reconstruction techniques should permit better evaluations of the consequences of future changes in snow and ice cover and temperatures in Arctic lakes following proposed climate changes.

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Influence of fishers' behaviour on the catchability of surface tuna schools in the Venezuelan purse-seiner fishery in the Caribbean Sea

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Abstract: The influence of Venezuelan skippers' behaviour on the catchability of surface tuna schools was modelled using logistic regressions. Data obtained from observers onboard purse seiners indicated that fishers' fine-scale decisions, such as chasing and setting a school, were influenced by (*i*) the skipper's skill, (*ii*) the fishing equipment used (e.g., whether a bird radar was used or not), (*iii*) the features of the tuna school, and (*iv*) some environmental factors. The connections among the decisions related to the fishing process and these variables were synthesized in a causal network approach. Results clearly showed that schools (*i*) composed by fishes under 2 kg and (*ii*) where biomass was lower than 5 metric tons were disregarded by fishers. Because fishers used these thresholds to decide when to set the net, modifications in their behaviour over the years may introduce serious biases in the analysis of any catch rate and abundance relationship. An average daily activity record of a purse seiner shows the proportion of time spent in searching and in setting activities and highlights the impact that the use of new fishing equipment may have on fishing power.

Résumé : L'impact du comportement des capitaines vénézuéliens sur la capturabilité des bancs de thons en surface a été modélisée à l'aide de régressions logistiques. Les données recueillies par des observateurs à bord des senneurs, permettent de relier les décisions des pêcheurs, telles que la poursuite du banc et le coup de filet, (*i*) au savoir-faire du capitaine, (*ii*) à l'utilisation de certains équipements technologiques (par ex., le radar à oiseaux), (*iii*) aux caractéristiques du banc de thons et (*iv*) à quelques facteurs environnementaux. Les relations entre les décisions impliquées dans le processus de pêche et ces facteurs ont été synthétisées à l'aide d'un réseau causal. Ce travail met clairement en évidence que les bancs (*i*) composés d'individus de moins de 2 kg et (*ii*) de biomasse inférieure à 5 tonnes étaient délaissés par les pêcheurs. L'existence de ces seuils dans la décision de tenter le coup de filet signifie que toutes modifications du comportement des pêcheurs au cours du temps pourra introduire de sérieux biais dans l'analyse des relations entre les rendements et l'abondance. Un résumé de l'activité journalière d'un senneur met en évidence le temps passé lors des phases de recherche du poisson et de sa capture et souligne le rôle des nouveaux équipements dans l'augmentation des puissances de pêche.

Introduction

Tunas are highly migratory species that need to move continuously between suitable habitats to find the best environmental conditions for their development. Considering the range of the fishing grounds, tuna densities appear very weak comparatively with other species. For instance, the density of the three main species of tunas caught in the tropical Atlantic Ocean was estimated to be near 250 kg/mi^2 (1 mi^2 = 2.6 km^2) (Fonteneau 1989). At first glance, it may be dubious that any tuna fishery could be economically sustainable if tunas were uniformly distributed throughout their potential distribution area. Nevertheless, the environmental discontinuities in space and in time favour the aggregation of tuna schools in patches (i.e., concentrations). For this reason, and considering the costs of purse seiners, locating and exploiting these ephemeral patches with efficacy is a necessity in maintaining this type of fishery at an economically sustainable level.

Information on effort and catch per unit of effort is essential for stock assessment, and to obtain this, it is necessary to have a thorough understanding of fishing effort. Fishing effort (f) has traditionally been related to fishing mortality (F) by the relationship $F = qf$, where q is the catchability coefficient. Catchability can be divided into components that depend on the behaviour of fishes, such as vulnerability and accessibility, and the component related with fishers' efficiency. Fishing effort itself is related to the physical charac-

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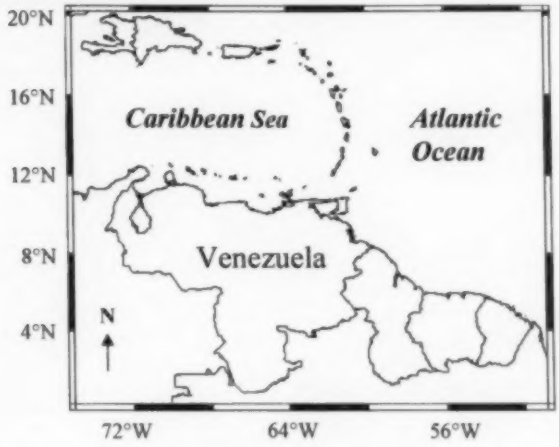
Fig. 1. Map showing the location of the study area off the Venezuelan coast.



teristics of the boats and their fishing equipment and also the skippers' skill. For schooling pelagic species, it is particularly important to identify factors that modify fishers' strategies, since otherwise, changes in the catch rates will be interpreted only as changes in abundance. In the same way, good fishery management should take into account the fishers' behaviour and their decision-making mechanisms (in an attempt to understanding when, where, how, and why they choose to operate) before establishing regulations (Hilborn and Walters 1992).

The way in which a captain decides how to exploit these concentrations during the year leads to concepts such as fishing strategy and fishing tactics (Laloë and Samba 1991; Ferraris 1995). Both concepts can be considered as fishers' behavioural responses against uncertain events found in the ecosystems at different spatial and temporal scales. A tactic is a fine-scale response, whereas a strategy represents a more planned reaction in time and space. The strategies adopted by Venezuelan purse seiners, with respect to the usefulness of the aid brought by a bait boat during the set, were examined by Gaertner et al. (1996). In contrast, the aim of the present analysis is to identify factors that affect skippers' fine-scale decisions (i.e., chasing and setting a school) and to analyze their impact on the catchability of surface tuna schools.

The Venezuelan surface tuna fishery (bait boats and purse seiners) became fully developed in the early 1980's after exploratory fishing in early 1972 (Mihara et al. 1972). The major part of the catches (mainly yellowfin tuna (*Thunnus albacares*) and skipjack tuna (*Katsuwonus pelamis*)) were made in the southern Caribbean Sea and in the adjacent areas of the western Atlantic Ocean (Gaertner et al. 1989). After a maximum of 45 000 metric tons (t)/year, reached in 1983–1984, catches decreased sharply as the result of relocation of the majority of fishing effort of large purse seiners to the eastern Pacific Ocean. Today, catches in the Atlantic Ocean fluctuate between 25 000 and 30 000 t and the entire current Venezuelan fishing grounds are from about 8 to 14°N and from 57 to 71°W (Fig. 1).

One of the major features contributing to the success of purse seiners' activities is the presence of a shallow mixed layer marked by a sharp gradient (Green 1967). In the Venezuelan sector the deepening of the thermocline and of the oxycline to the north limits the areas with suitable conditions for surface tuna fishery to the southeastern margin of the Caribbean Sea (Gaertner et al. 1989). When a tuna school is chased, the skipper of the purse seiner can decide to enlist the assistance of a bait boat (pole-and-line fishing) to improve the probability of a successful set. The bait boat throws the live bait overboard (e.g., *Sardinella* spp.) to hold tuna schools stationary near the surface during the encircling operation of the purse seiner. A percentage of the total catch of the set is shared with the bait boat (33% if both vessels belong to the same company and 25% otherwise). Tuna fishers know that surface-swimming tuna schools tend to concentrate under floating objects or under marine animals. In this part of the Atlantic Ocean, although nonassociated schools (namely, school sets) were the predominant fishing mode as reported in logbooks, a high proportion of sets were made in the presence of whale sharks (*Rhincodon typus*) or in the presence of whales. In contrast the percentage of sets made on flotsam (logs) is very low (Gaertner et al. 1996). Nonassociated schools are signalled by the presence of bird flocks or by the disturbance of the water when tunas are feeding.

Materials and methods

Data

The seven purse seiners that received observers aboard (among the 10 vessels fishing continuously in the Caribbean Sea) belonged to Venezuelan companies operating from Cumana (Sucre) and varied in carrying capacity from 250 to 900 t. The observers' trips were made on an opportunistic basis from August 1992 to November 1994 and were limited to 16 for financial reasons (corresponding to 505 days at sea). The data were collected mainly from the Venezuelan coast to 14°N and from the lesser Antillean Islands in the east (about 60°W) to the Colombian waters in the west (about 71°W). Because the fishing grounds are near the equator, dawn and dusk were standardized to 06:00 for sunrise and 18:00 for sunset.

Records were made every 2 h, even in the absence of detection (time of day, position, speed of the vessel, weather at sea, use of bird radar, etc.) or each time a sighting was made. In the latter case, the nature of the event, the sighting distance, the sighting angle (from the trackline), and the response of the skipper (pursuit or not) were registered. If the pursuit broke off without the net being launched, the reason(s) was (were) noted (including, at times, the estimated size of the school and the estimated size category of fishes). When the chase continued, information on the set was also recorded (e.g., catch aboard, discards, proportion of estimated escapement, species and weight composition, time spent in the different parts of the fishing operation). Of the 853 events registered, 308 were followed by the net being set.

To correct the observer's bias in school size estimates, bias adjustments were performed from schools in which an initial estimate (C_{obs}, made before the set) was followed by a best estimate (C_{set}, when the school was set upon). The sets in which observers noted escapement were not included in this calculation. The observer's initial estimate was then adjusted by multiplying it by the correction factor a, where $a = \Sigma C_{set} / \Sigma C_{obs}$. The bias adjustment (0.84) was similar to crews' bias estimates found in the eastern Pacific (Buckland and Anganuzzi 1988).

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Model development

Multiple logistic regression is frequently used to build models that predict the probability of a binary response ($y_i = 0$ for nonresponse and $y_i = 1$ for response) as a function of a set of explanatory variables x_i. The logistic regression function assumes that the conditional mean of y_i, given a set of x_i, can be formulated as

$$E(y_i|x_i) = \pi(x_i) = \text{Prob}(y_i = 1|x_i) = \frac{\exp(\beta_0 + \sum \beta_i x_i)}{1 + \exp(\beta_0 + \sum \beta_i x_i)}$$

where x_i is the covariate vector and β_i is the unknown coefficient vector.

Logistic regression is a special case of generalized linear models (GLM) with the logit link function $g(x_i) = \log[\pi(x_i)/(1 - \pi(x_i))] = \beta_0 + \Sigma\beta_i x_i$ (Hosmer and Lemeshow1989; Agresti 1990). The odds ratio is more easily interpretable than the estimated coefficient (β). It summarizes net impacts of predictors by indicating the multiplicative impact on the odds for a unit increase in a given predictor, net of all other covariates in the model (Agresti 1990). The odds ratio (ψ) is

$$\psi = \frac{P(\text{response}/x = 1)/P(\text{nonresponse}/x = 1)}{P(\text{response}/x = 0)/P(\text{nonresponse}/x = 0)}$$

where P(response/x = 1) is the proportion of events that lead to a response (for instance, a pursuit), given that the explanatory variable x = 1.

Variable selection

For representing the probabilities that a fisher takes decisions such as "to pursue a school" and "to set a school" (the dependent variables in this study), the first step consisted in selecting a subset of variables among a list of candidate ones. For each candidate variable, the hypothesis that the slope coefficient is zero is tested with the use of the likelihood ratio test. Hosmer and Lemeshow (1989) recommended that any candidate variable whose univariate test has a p value <0.25 be retained for the multivariate model selection. For continuous variables identified as important, the assumption of linearity in the logit was checked with the aid of the Box–Tidwell transformation (see Hosmer and Lemeshow 1989, p. 90). For the variables transformed as a categorical factor, a new assessment of linearity in the logit was made.

Model selection

The aim in model building is to reach a trade-off between the extremes of underfitting the data (too little structure, which means large bias) and overfitting the data (too many parameters, hence large variance). With the above consideration in mind, the concept of the principle of parsimony (McCullagh and Nelder 1983) is based on the search for the number of parameters that minimizes both functions of bias and variance (see fig. 1 in Burnham and Anderson 1992).

The stepwise selection procedure has widely been used to build models in linear regression. A simple model can be used and significant variables are added (forward selection), or, by contrast, from a fully parameterized model, the nonsignificant factors are excluded (backward elimination). This framework still has some disadvantages: (*i*) the cost in time of computation because the coefficients for all variables (included or not in the model) must be estimated at each step, (*ii*) these two approaches do not converge necessarily to the same final model, (*iii*) multiple tests are made for the same data set and the effective α level of the tests is greater than the nominal α level fixed a priori for a single test, and (*iv*) the successive comparisons are restricted to nested models (because the selection is based on the likelihood ratio test). On the basis of these arguments, the use of Akaike's information criterion (AIC) in likelihood contexts has been suggested to reduce model building strategy to a one-dimensional optimization problem emphasizing parsimony (Burnham and Anderson 1992; Lebreton et al. 1992): AIC = –2(log-likelihood) + 2K, where K is the number of parameters in the model. The model with the smallest AIC is defined as the parsimonious model. Once an adequate model is selected, the neighbouring nested models are checked with the help of the likelihood ratio test to detect whether important factors (including interactions) are necessary.

Goodness-of-fit and diagnostics for influential observations

The overall measures of fit are assessed by the Hosmer–Lemeshow statistic (C), and other diagnostics, derived by Pregibon (1981), are used to identify respectively outliers and influential observations. The methodology to assess goodness-of-fit and coefficient sensitivities is based on changes in value of (*i*) the Pearson chi-square statistic $\Delta\chi_j^2$, (*ii*) the deviance ΔD_j, and (*iii*) the coefficient vector $\Delta\beta_j$, after deleting each observation (see Hosmer and Lesmeshow 1989, pp. 149–170).

The use of a prediction success table built with the same data set that is used to develop the model can give optimistic results. It is good practice to check the correct classification of the observations with the help of an independent data set. As a general rule, the original data set is randomly divided into two parts: the larger subset is used to develop the model (learning sample) and the second one is retained to do the verification process. Although, in practice, the calibration–verification method is not subject to the optimistic bias, three disadvantages have been raised by Prager and Fabrizio (1990): (*i*) the relatively large sample required, (*ii*) the possibility that the selected models could be different between the calibration subset and the complete data set, and (*iii*) the problematic choice for the size of the verification sample (e.g., a large holdout sample gives a good estimate of the model's performance but a poor estimate of the "best" model itself, and reciprocally). Bearing in mind that in the present study the main objective was not to predict future events but to identify factors affecting fishers' decisions, the use of the complete data set was preferred to the calibration–verification method. The calculations were performed with the use of the LOGIT module of the SYSTAT package (Steinberg and Colla 1991).

Results

Factors affecting the decision to chase a school

The list of candidate variables analyzed to predict the pursuit of a school included the sighting angle (A, scaled to 0–180°), the sighting distance (D), the nature of the sighting (I_1 = nonassociated school, I_2 = whale shark, I_3 = whale, I_4 = others, I_5 = another boat), the time of day ($H_1 \leq$ 09:00, H_2 = 09:00–12:00, H_3 = 12:00–15:00, $H_4 >$ 15:00), the trip skipper identification (T = 1, ..., 7), the use of bird radar (R = yes/no), the percentage of filled wells over the trip (considering that the carrying capacity of the vessel equals 100%; Fd_1 = 0%, Fd_2 = 1% – 20%, $Fd_3 >$ 20%), an unsuccessful previous set (U = yes/no), no catch during the previous day (C = yes/no), the visibility (V), the weather at sea (i.e., height of the waves in metres: $Sd_1 \leq 1$, $Sd_2 > 1$), and the cloud cover (K). Because Fd represents the cumulative percentage of tuna stored in the wells over the trip (whereas C only represents the catch done the previous day), we assume that collinearity between Fd and C is weak.

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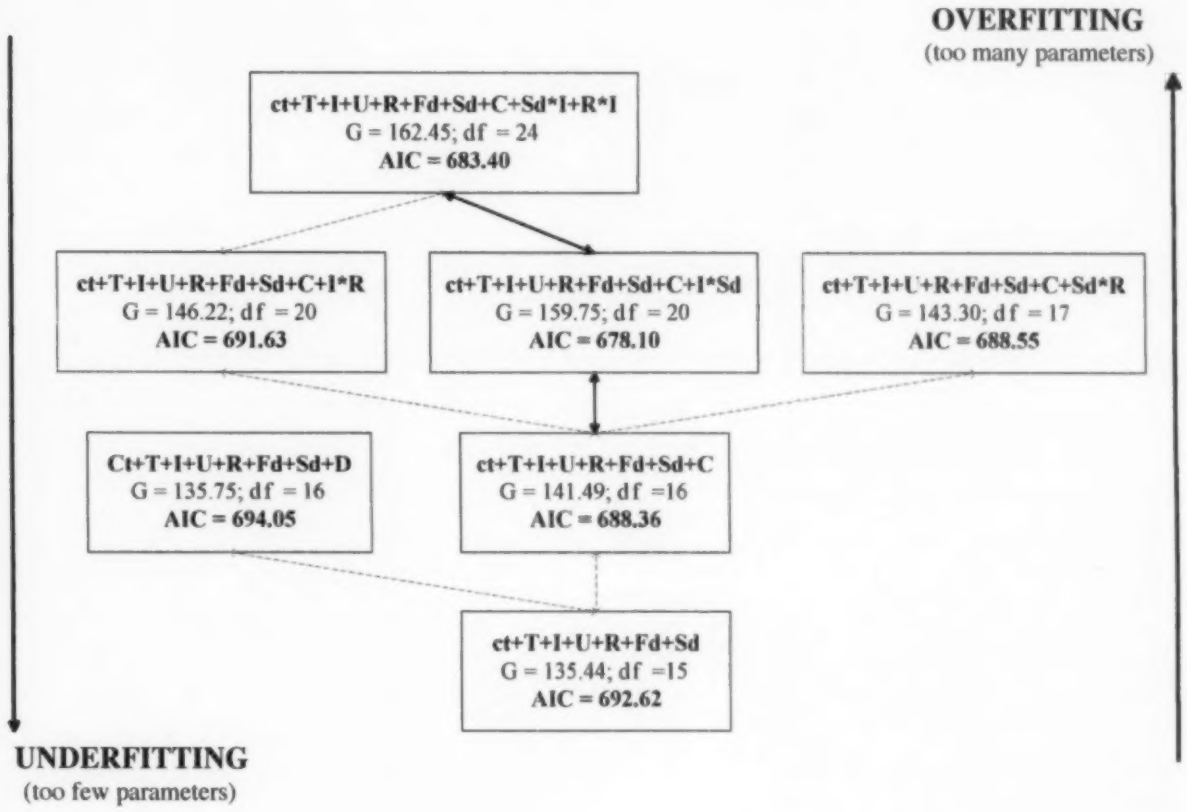
Fig. 2. Representation of the selection pattern of logistic models used to fit the decision to chase a school. *G*, likelihood ratio test statistic; AIC, Akaike information criterion. Explanatory variables were trip skipper (*T*), sighting index (*I*), unsuccessful previous set (*U*), zero catch the day before (*C*), use of bird radar (*R*), weather at sea (Sd), filling rate of the boat (Fd), and sighting distance (*D*). The parsimonious model was obtained for logit P = ct + T + I + U + R + Fd + Sd + C + I·Sd; hence, only two tests were performed (solid double-headed arrows). The arrows on the left and right sides of the figure represent the trade-off between the extremes of underfitting and overfitting.



The highly significant variables ($p < 0.001$) were the trip skipper (*T*), the sighting index (*I*), the filling rate of the boat (Fd), the use of bird radar (*R*), the weather at sea (Sd), and an unsuccessful previous set (*U*). The distance from the vessel to the event detected (*D*), the visibility (*V*), and, perhaps, zero catch the previous day (C) presented some interest ($p < 0.25$). Considering that visibility affects more likely the probability of detecting a sighting index than the decision to chase a school and to prevent potential collinearity with the weather at sea, visibility was not retained. Once the set of explanatory variables was identified, the multivariate analysis was formed with the main effects and "only with interactions which make biologic sense" (Hosmer and Lemeshow 1989). Since trips were made on an opportunistic basis, the resulting unbalanced designs did not permit a direct appreciation of the skipper effect. The variable trip skipper (*T*) gathered observations made with the same vessel and the same captain, but reflected also spatial and temporal effects (the dichotomization of these two factors would create too many zero cells, which are manifested by extraordinarily large estimated standard errors). The smallest AIC statistic was reached for logit P = ct + T + I + U + R + Fd + Sd + C + I·Sd (Fig. 2). At this step of the model building procedure, only two likelihood ratio tests were performed. The *G* test for the inclusion of the I·R interaction was nonsignificant ($\Delta G = 2.706$ for 4 df, $p = 0.608$). In contrast, the inclusion of the I·Sd interaction provided a significant improvement over the model built only with main effects ($\Delta G = 18.255$ for 4 df, $p = 0.001$). In conclusion the analysis yielded seven main factors (the trip skipper effect, the sight-

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Table 1. Estimated coefficients (β), estimated standard errors, t ratios, p values, odds ratios (ψ), and 95% confidence intervals (CI) for the multivariate model selected to assess the variability in the logit of the probability to pursuit a school.

Variable	β	SE	t	p	ψ	Upper CI	Lower CI
Constant	–0.320	0.795	–0.402	0.688			
Trip_1	–0.345	1.057	–0.326	0.744	0.708	5.622	0.089
Trip_2	–0.378	0.809	–0.468	0.640	0.685	3.345	0.140
Trip_3	2.306	0.675	3.418	0.001	10.035	37.654	2.674
Trip_4	0.408	0.705	0.578	0.563	1.503	5.984	0.378
Trip_5	2.314	1.290	1.794	0.073	10.119	126.849	0.807
Trip_6	0.417	0.929	0.449	0.653	1.518	9.384	0.246
Sight_index_1	2.788	0.676	4.122	<0.001	16.244	61.138	4.316
Sight_index_2	1.754	0.438	4.005	<0.001	5.776	13.624	2.448
Sight_index_3	0.521	0.410	1.270	0.204	1.684	3.762	0.754
Sight_index_4	1.037	0.394	2.630	0.009	2.821	6.110	1.302
Fillingd_1	0.399	0.313	1.273	0.203	1.490	2.755	0.806
Fillingd_2	1.679	0.435	3.857	<0.001	5.358	12.572	2.283
Unsuccessful_set	0.749	0.405	1.850	0.064	2.116	4.681	0.956
Zero_catch	0.356	0.241	1.480	0.139	1.428	2.290	0.891
Bird radar	–1.883	0.521	–3.614	<0.001	0.152	0.422	0.055
Weather at sea	–0.793	0.319	–2.484	0.013	0.452	0.846	0.242
Sight_index_1·weather at sea	–0.720	0.911	–0.790	0.429	0.487	2.904	0.082
Sight_index_2·weather at sea	0.703	0.687	1.023	0.306	2.020	7.764	0.525
Sight_index_3·weather at sea	2.221	0.805	2.758	0.006	9.212	44.650	1.901
Sight_index_4·weather at sea	2.947	1.142	2.581	0.010	19.055	178.663	2.032

Note: All variables were treated as categorical.

ing, an unsuccessful previous set, whether a bird radar was used or not, the filling rate of the boat, the weather at sea, no catch during the previous day) and one interaction (the sighting index with the weather at sea) that had a significant impact on the chasing.

After regression diagnostics, 53 records were deleted. The reduced data set was fitted with the same best model. McFadden's Rho^2, which mimics an R^2 coefficient, was improved (0.241, C = 6.677 for 8 df, p = 0.572). Of a total of 693 events observed, 73% were correctly classified. Chasing a school was successfully predicted at 83% by the selected logit model. Nevertheless, the success index (i.e., the gain that this model exhibits in correct prediction over a purely random model) was relatively low (6%). This statistic was better for the decision to abandon the pursuit (19%).

Categorical variables in this analysis were set up such that all levels were contrasted with a reference level to ensure that the design matrix was of full rank. For instance, the estimated coefficients (β) for each level of the variable sighting index (I) represent the log of the odds (ψ), using nonassociated school as reference level (I_1). The estimated coefficients for this variable were respectively $\log[\psi(\text{whale shark, nonassociated})] = 2.79$, $\log[\psi(\text{whale, nonassociated})] = 1.75$, and so on (Table 1). The corresponding odds ratio and the confidence intervals (CI) were obtained directly by exponentiation, $\psi = \exp(\beta)$ and $CI = \exp[\beta \pm z_{1-\alpha/2} \cdot SE(\beta)]$. When the interval for ψ did not include 1, the probability of a response was significantly associated with the presence of the discrete variable. Thereby, we concluded that the decision to pursue a school occurred twice as often when the previous set was unsuccessful than when it was successful. The odds ratio of the pursuit increased slowly when no tuna school had been caught during the previous day, but was five times higher when the filling rate was beyond one fifth full. In contrast, the use of bird radar seemed a deterrent for the decision to chase a school. The occurrence of a pursuit was about 2/13 less frequent among the skippers who used this fishing gear than among those who did not. Although nonsignificant at the 0.1 level, the variable zero catch the previous day was kept (p = 0.139) because its influence on the probability to pursue a school was assumed likely. It can be argued that the significance of the trip skipper effect is mainly due to Trip_3 (with respect to the reference level). Nevertheless, (*i*) a trip skipper effect is a priori likely in a surface tuna fishery and (*ii*) taking into account this effect improves the estimates of the other causes of variability. The presence of an interaction between the sighting index (I) and the weather at sea (Sd) meant that the effect I on the outcome variable depended on the level taken by Sd, and reciprocally. In evaluating the corresponding odds ratios, we considered first the estimated logit for a situation in which Sd and I take a determined level, holding the remaining variables constant (see Hosmer and Lemeshow 1989, pp. 102–104). The logit differences were computed only among I in function of the level taken by Sd (Table 2). When the waves were higher than 1 m, the likelihood of a pursuit decreased for school sets and for schools associated with whale sharks (in contrast, the pursuits increased for mixed events and for schools detected by another boat).

Factors affecting the decision to launch the net

Among the reasons reported by observers, 34% (60 events) of the pursuits not ending by a set were caused by the skippers' decisions and 39% (69 events) by the tuna schools' behaviour (Table 3). It was impossible to perform the logistic model in some situations due to the fact that no

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Table 2. Estimated logit differences, odds ratios (ψ), and 95% confidence intervals (CI) for the effect of the variable weather at sea among the different sighting indices.

Sighting index	Logit difference	ψ	Upper CI	Lower CI
Nonassociated	–0.793	0.452	0.846	0.242
Whale sharks	–1.513	0.220	1.248	0.039
Whales	–0.090	0.914	3.287	0.254
Others	1.428	4.170	19.277	0.901
Called by a boat	2.154	8.619	77.132	0.963

sets were tried (i.e., $Y = 0$). This was the case when the school dived before a set or when it moved faster than the vessel. In these situations, usually no guess as to the size of the school and the commercial size category of the fishes was recorded. The corresponding fitted logistic regression models would result in infinite odds ratios and very large estimated standard errors. In this study the help brought by a bait boat is suspected to have a large influence on the decision to set a school (Gaertner et al. 1996). However, because it was always associated with an attempt (i.e., $Y = 1$), the maximum likelihood estimates do not exist.

From the univariate analysis, the most significant factors ($p < 0.01$) were the commercial size category of the fishes ($W_1 \leq 2$ kg, $W_2 = 2$–10 kg, $W_3 > 10$ kg), the size of the school ($Z_1 \leq 5$ t, $Z_2 = 5$–10 t, $Z_3 > 10$ t), the trip skipper (T was reduced to 1,..., 4 because we considered only records in which the school size and the fish category were estimated), the filling rate of the wells (Fd), an unsuccessful set during the previous attempt (U), and a zero catch the day before (C); the sighting effect (I) was less significant ($p < 0.10$). In contrast, there were no clear patterns of differences between the categories of the vessel speed (Sv), the duration of the pursuit (Hp), or the weather at sea (Sd) according to the occurrence of whether these factors led to a set or not. The G test for the inclusion of the sighting index (I) into the parsimonious model, logit $Y = \text{ct} + T + U + C + \text{Fd} + Z + W$, was nonsignificant ($\Delta G = 5.768$ for 4 df, $p = 0.217$). Nonetheless, considering that (*i*) fishers know a priori the influence of this variable on the success of a set and (*ii*) that the sighting index was important in determining the probability of pursuing the school (the previous decision to occur), the sighting index was retained. Hence the setting was dependent on the trip skipper effect, an unsuccessful previous set, no catch during the previous day, the filling rate of the vessel, the school size, the size category of the fishes, and the sighting index. After elimination of outliers, McFadden's Rho^2 statistic increased from 0.395 to 0.463 ($C = 4.919$ for 8 df, $p = 0.776$). Of the 204 observations, 77% were correctly allocated by the predictive model. The success index equaled 20% for the decision to set the net and 32% for a nonresponse.

The great impact of the size category of the fishes (W) and the size of the school (Z) was highlighted. For instance, the odds of setting the net were multiplied by 30 when the size category was the medium or the large one (with respect to schools composed of small fishes; Table 4). The likelihood to set on a school larger than 10 t was eight times higher than for the small school size, but only 2.7 times higher for a 5- to 10-t school size. When the filling rate of the boat was high (as seen at the end of the trip) the odds of setting the net increased, whereas zero catch the day before provided a decrease.

Table 3. Events associated with a pursuit not ended by a set (for a subset of 178 records correctly registered by observers aboard).

Event	*n*	%
Decision of the skipper		
School size too small	36	20.2
Low weight of the fish	22	12.4
Small tuna species	2	1.1
Subtotal	60	33.7
Behaviour of the tuna school		
Moved too fast to be stopped	42	23.6
Refused the bait	3	1.7
Dive before the set	23	12.9
Detected by a sonar (too deep)	1	0.6
Subtotal	69	38.8
Other		
Sightings without fish	42	23.6
Miscellaneous	7	4.0
Subtotal	49	27.6

Factors influencing the success of the set

In this study, all sets of 1 t or more are termed successful. The candidate explanatory variables were the sighting index (I, reduced to school sets, whale sharks, and whales), the trip skipper effect ($T = 1,..., 5$), the assistance of a bait boat (A = yes/no), the unsuccessful previous set (U), the weather at sea (Sd), the school size (Z), the size category of the fishes (W), the cloud cover (K), and the time of day (H). A previous study has shown that some variables (such as the sighting) could interact with the assistance of the bait boat on the success of the set (Gaertner et. al. 1996). For this reason, the effect of each candidate variable was checked in relation to its respective interaction with A. The parsimonious model was obtained from logit $N = \text{ct} + A + I + T + Z + W + A{\cdot}I + A{\cdot}T$. The G test for the inclusion of the $A{\cdot}W$ interaction was not significant ($\Delta G = 0.81$ for 2 df, $p = 0.666$). After elimination of some outliers (four items), a new fit was done (McFadden's $\text{Rho}^2 = 0.289$, $C = 7.950$ for 8 df, $p = 0.438$). Seventy-five percent of the observations were well allocated by the model. The success index was especially good for the rate of unsuccessful sets (25%). The unsuccessful sets are more likely for sets made on schools larger than 5 t, and especially for sets made on the 5- to 10-t class. Considering the size category of the fishes, the odds ratio of having an unsuccessful set was lower for the medium class (relative to the small fishes) but increased significantly for large tunas (Table 5).

Discussion

Factors affecting catchability, such as fishing power of the vessels and (or) skippers' skill, are used in fishery research *to describe what things are happening*, but not always *to understand why things are happening*. At-sea observers' data are helpful in explaining the temporal scheduling of the events related to the fishing process, such as chasing a school, setting the net, and having a successful set. Ex-

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Table 4. Estimated coefficients (β), estimated standard errors, *t* ratios, *p* values, odds ratios (ψ), and 95% confidence intervals CI) for the multivariate model selected to assess the variability in the logit of the probability to set a school.

Variable	β	SE	*t*	*p*	ψ	Upper CI	Lower CI
Constant	–2.106	1.094	–1.924	0.054			
Trip_1	–2.186	0.626	–3.491	<0.001	0.112	0.383	0.033
Trip_2	–0.560	0.709	–0.790	0.430	0.571	2.293	0.142
Trip_3	2.637	1.273	2.072	0.038	13.972	169.313	1.153
Sight_index_1	–0.458	0.709	–0.646	0.518	0.633	2.536	0.158
Sight_index_2	–2.242	0.767	–2.923	0.003	0.106	0.478	0.024
Sight_index_3	–0.420	0.817	–0.514	0.608	0.657	3.262	0.132
Sight_index_4	0.127	0.670	0.190	0.849	1.136	4.225	0.305
Fillingd_1	0.729	0.717	1.018	0.309	2.073	8.445	0.509
Fillingd_2	1.400	0.836	1.675	0.094	4.055	20.862	0.788
Sizecal_1	1.011	0.629	1.608	0.108	2.748	9.423	0.801
Sizecal_2	2.073	0.582	3.565	<0.001	7.952	24.861	2.543
Weight_1	3.405	0.836	4.076	<0.001	30.129	154.957	5.858
Weight_2	3.412	0.893	3.820	<0.001	30.325	174.630	5.266
Unsuccessful_set	0.540	0.600	0.899	0.369	1.715	5.561	0.529
Zero_catch	–1.259	0.594	–2.118	0.034	0.284	0.910	0.089

Note: All variables were treated as categorical.

plaining means linking one fact with others, in other words, making the whole description intelligible. It is obvious that concatenating fishing factors with fishers' decisions is not easy. The cause of any particular skipper decision can be multiple and conjectural. Furthermore, effects of multiple causes are not the same in all surface tuna fisheries, and different combinations of causes can turn out to have similar effects. For these reasons, we do not claim to predict future skippers' decisions, but only to show how some choices can be linked with the occurrence of certain prior events.

In order to represent connections among dependent and independent variables, we used a causal network approach (Fig. 3). The influence of an independent variable was evaluated with the likelihood ratio test between the selected model and the same model without this variable. The trip skipper effect, the filling rate of the vessel, the nature of the sighting, the interaction between the sighting and the weather at sea, and the use of bird radar are involved in the transition from searching to chasing (Fig. 3). The fact that cloud cover was not found as being a significant predictor of the chasing decision suggested that its impact was limited to the probability of detecting a tuna sensor. How fishers take the decision to launch the net was strongly dependent on the trip skipper effect, the sightings, the school size, and the commercial size category of the tunas. All the variables indicating prior successes had a weak effect on the chasing and on the setting. With respect to the success of a set, the interaction between the trip skipper effect and the assistance suggested that the manner in which a skipper uses the assistance of a bait boat was more important than his own ability to fish. The size category of tunas in the school had a large influence on this probability.

Several improvements have been made in fishing equipment to increase the fishing power of purse seiners over the years. Other changes that affect catchability include variations in the vulnerability of tuna schools and modifications in fishers' behaviour. Since there is little detailed information on the date of introduction of fishing devices by vessel, trends in catch per unit of effort might be confounded with improvements in the fishing equipment or with changes in behaviour associated with the introduction of new technology. A summary of the potential biases in the relationships between catch rates and abundance due to these factors is provided in the following subsections.

Factors linked with the fishers' skills and their efficiencies

It is obvious that the skipper's skill is an important factor in the fishing efficiency of any tropical surface tuna fishery. Although it is likely that the strong influence of the trip skipper effect on the chasing and setting decisions (Fig. 3) is due more to the efficiency and the skipper's skills rather than to time and area interaction (because the study area is relatively small, Fig. 1), the latter cannot be eliminated. Fishers' temperament can be related to spatial and temporal effects, especially for fishers characterized as movement specialists. These skippers, who often use large vessels in better condition, prefer following their target from one area to another rather than staying in a particular area (area specialists). Both strategies are found in numerous fisheries (Hilborn 1985; Laloé and Samba 1991; Gaertner et al. 1996). Another important factor is the cooperation developed within subgroups of vessels formed between friendly skippers (code groups) and how information is shared between fishers in order to locate as fast as possible a new concentration of schools. Unfortunately, both components are difficult to integrate into a catch rate analysis.

Some lagged variables, such as the filling rate of the wells or no catch the day before, might affect the skipper's motivation. The increased motivation caused by the filling rate of the wells could be related to the success in localizing patches. Once the skipper had found a concentration, an increased responsiveness was seen in many cases. In the same way, at the beginning of the trip, when expectations of better findings existed, the skipper's disregard of small schools may have been motivated only by larger ones (Freon 1991).

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Table 5. Estimated coefficients (β), estimated standard errors, t ratios, p values, odds ratios (ψ), and 95% confidence intervals (CI) for the multivariate model selected to assess the variability in the logit of the probability of an unsuccessful set.

Variable	β	SE	t	p	ψ	Upper CI	Lower CI
Constant	–3.403	2.365	–1.439	0.150			
Trip_1	1.790	2.172	0.824	0.410	5.991	423.140	0.085
Trip_2	2.463	2.136	1.153	0.249	11.745	772.941	0.178
Trip_3	1.009	2.131	0.474	0.636	2.743	178.823	0.042
Trip_4	1.006	2.366	0.425	0.671	2.736	282.667	0.026
Assistance	–2.018	2.598	–0.777	0.437	0.133	21.646	0.001
Sight_index_1	–0.211	1.062	–0.199	0.843	0.810	6.489	0.101
Sight_index_2	0.983	1.192	0.825	0.409	2.674	27.632	0.259
Sizecal_1	1.991	0.906	2.198	0.028	7.324	43.233	1.241
Sizecal_2	1.379	0.865	1.595	0.111	3.970	21.617	0.729
Weight_1	–1.273	0.622	–2.048	0.041	0.280	0.947	0.083
Weight_2	2.664	1.196	2.227	0.026	14.360	149.810	1.377
Sight_index_1·assistance	1.278	1.320	0.969	0.333	3.591	47.686	0.270
Sight_index_2·assistance	–1.057	1.458	–0.724	0.469	0.348	6.061	0.020
Trip_1·assistance	1.553	2.517	0.617	0.537	4.728	655.949	0.034
Trip_2·assistance	–4.050	2.777	–1.459	0.145	0.017	4.020	0.000
Trip_3·assistance	2.018	2.674	0.755	0.450	7.527	1422.359	0.040
Trip_4·assistance	0.923	2.749	0.336	0.737	2.517	550.709	0.012

Note: All variables were treated as categorical.

As a result, it appears that the opportunity cost associated with the decision to set the net is a considerable one (Hancock et al. 1995).

Factors linked with the fishing equipment of the boats

The main effect of the use of bird radar is the increase in the effective searching area, which leads to an increase in the encounter rate. Depending on different density levels and aggregation rates, some simulations made by Marsac (1991) suggested that the vessel's searching capacity could be multiplied by a factor of 3–9. For this reason, the assumption that bird radar was one of the causes of the increasing fishing power observed in the eastern Atlantic tuna purse-seiner fishery was made by Gascuel et al. (1993). Direct effect of the use of bird radar was also reported in the bait boat Ghanean fishery (Kwei and Bannerman 1993). In the present study, it was only noted whether the bird radar was used or not, and not whether each event was detected with this gear. In practice, it was very difficult for an observer aboard to estimate (*i*) whether a given school was directly found by using bird radar or, in contrast, (*ii*) whether it was detected by binoculars after the bird radar was used first to locate a patch. The bird radar fishing equipment had a deterrent effect on the decision to chase a school, despite the fact that the percentage of nonassociated schools increased when it was in use (also reported in the eastern Atlantic Ocean, Hervé et al. 1991). Judging from these examples, bird radar would be, above all, useful for localizing tuna patches. This is supported by the fact that once sighted, the vessel travels toward the concentration and the crew uses binoculars to scan the surface of the sea searching for other signs that indicate the presence of tunas. At this point, bird radar would be used only to disregard unsuitable events (e.g., explaining why a "negative" effect on the chasing activity was found).

Use of sonar is known to have influence in some pelagic fisheries but could not be checked in this study because data were incomplete. In the Chilean horse mackerel (*Trachurus murphyi*) purse-seiner fishery, Hancock et al. (1995) noted that echo sounders and side-scanning sonar are used to access the school density and size and then, just before the net is set, to estimate the size and direction of the school more accurately. Observers aboard the French tuna fleet operating in the eastern Atlantic and Indian oceans confirmed to us that sonar is used by skippers in order to decide whether or not the net will be launched (depending on the school size and its depth) and during the encircling operation (looking at where the school is moving).

During the last two decades, major changes in the purse-seiner nets have been made in order to reach deeper layers and to reduce the time devoted to hauling the nets. As a result, it is likely that factors such as net dimensions (depth and length), chains, or others devices used to increase the speed of submerging the net into the water and changes in the hauling power of purse winches and power blocks affected the fishing power of the vessels (Hervé et al. 1991; Hampton and Bailey 1992).

It was seen that the advantages of fast purse seiners are (*i*) the increase of the coverage of the searching areas, which may increase the encounter rate, and (*ii*) the capacity to pursue a school more easily than with a slow vessel (Pella and Psaropoulos 1975; Punsly and Deriso 1991). In the present analysis, there was no evidence that fast vessels could stop fast surface-swimming schools easier than slow vessels. This may be explained by the narrow range of the searching speed observed within Venezuelan vessels (only 9.5–12 kn).

Factors linked with the resource and the environment

It is known that factors affecting the catchability of the different tuna age groups include fishers' preference as well as the difference in vulnerability of these tuna categories. As mentioned in the Results section, 12% of the pursuits not ending in a set were attributed to the size category of the

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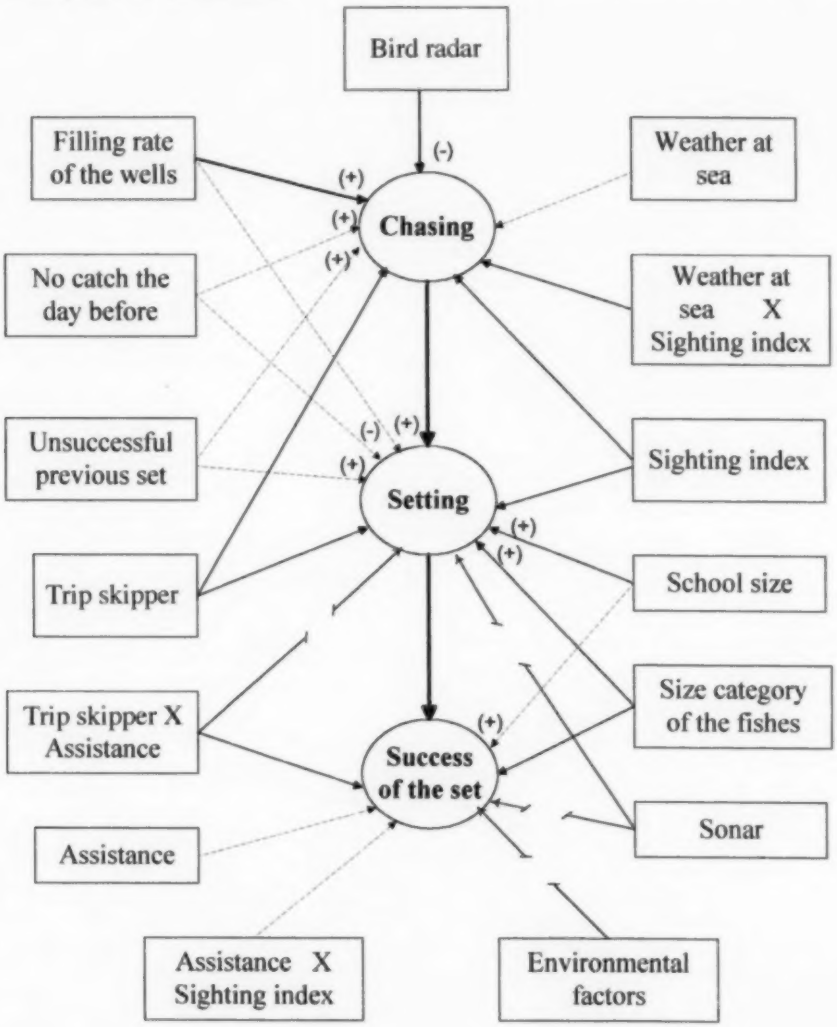
Fig. 3. Causal network activities of a purse seiner. weak causal influence ($p < 0.25$) (dashed arrows), strong causal influence ($p < 0.01$) (solid arrows), and influence likely but not tested in this study (arrows with a break). A plus sign (or a minus sign) means that the likelihood of a decision increases (or decreases) for a unit change in a given predictor (otherwise, it depends on the level of the categorical variable with respect to the contrast level).



fish being too low (Table 3). Most fishers prefer the largest tunas that they can find, especially when there is a large price differential. Hence, depending on variations in price and in abundance, temporary changes in the catch rates of the targeted size categories can be suspected. The present study has shown clearly that the decision to set the net increased when the school was composed of large fishes. The "corrected" probability of each size category was estimated with the coefficients obtained from the logit model. When the average weight of the fishes in the schools was lower than 2 kg, only 8% of the schools were hauled (Fig. 4A). Considering the occurrence of settings for the other two size categories (74 and 85%, respectively), the 2-kg limit can be considered as a threshold in the decision to set the net. In the Caribbean Sea, the small weight category includes juveniles of yellowfin and skipjack tuna as well as lower priced tunas, namely frigate tunas (*Auxis* spp.) or blackfin tuna (*Thunnus atlanticus*). A strong causal influence was also detected between the size category of the fishes and the success of a set (Fig. 3). The corrected probabilities of an unsuccessful set were respectively 17, 7, and 35% for the small, median, and large tuna categories (Fig. 4A). This means that, on average, large tunas (mainly yellowfin tuna) were twice as less vulnerable than small fishes and five time less vulnerable than medium fishes (yellowfin, skipjack, and blackfin tuna). However, the relatively low number of observations (n = 143) leads to careful interpretation of these results. Difference in vulnerability among the different size classes has been suggested for yellowfin tuna in the eastern Atlantic Ocean (Bard and Cayré 1986). Preadult yellowfin tuna

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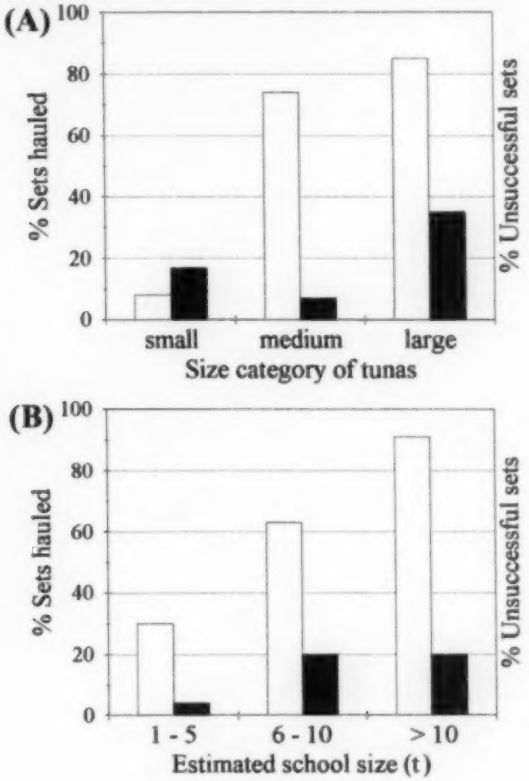
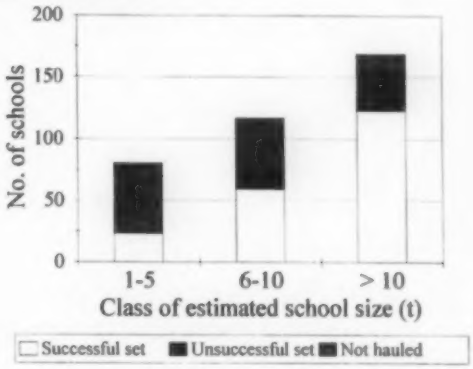
Fig. 4. Estimated percentages of sets hauled and estimated percentages of unsuccessful sets with respect to (A) the commercial size category of the fishes (small, ≤ 2 kg; medium, 2–10 kg; large, >10 kg) and (B) the estimated school size. Results provided by the logistic model showed clearly that tuna schools composed by fishes under 2 kg and whose biomass was lower than 5 t were disregarded by the Venezuelan fishers.



would be less vulnerable to purse seiners because they can form small schools (more difficult to catch or less interesting in total value).

Among the reasons given by the skippers in explaining why they broke off the pursuit, about 20% of them were attributed to a school size being too small (Table 3). The logistic model confirmed the strong influence of this factor on the decision to set the net. It appeared that tuna fishers were not reluctant to launch the net when the school size was larger than 10 t (91% of these schools were hauled, cf. Fig. 4B). This probability decreased to 63% for school sizes of around 5–10 t and to 30% for the smaller ones. At the same time, the corrected probability of an unsuccessful set was very low for the small schools (4 versus 20% for both larger sized schools). This suggests that Venezuelan fishers did not disregard the small schools for their lower vulnerability but preferred using their time to search for bigger schools. Likewise, this behaviour might change within the trip and over the years when abundances decrease. Such a situation (i.e., the necessity of catching smaller and smaller schools because larger ones are less frequently found) was

Fig. 5. Number of tuna schools per class of estimated school size (see text) corresponding to the observed successful sets, the estimated unsuccessful sets, and the estimated number of schools detected but not hauled.



mentioned for the artisanal sardine purse seiners of the Senegalese coasts by Freon (1991). Differences in strategies, according to the selection of school size, can also exist among the classes of tuna purse seiners. The small vessel class set on more small schools than did the larger ones (Pella and Psaropoulos 1975; Gaertner et al. 1996). As a result, modifications in fishers' behaviour and in set powers over the years might produce changes in catchability of tuna schools.

One of the key questions concerning the size of the school is the unknown proportion of biomass that escapes during a successful set (Pella and Psaropoulos 1975). The percentage of biomass caught for each class of school size was calculated as the ratio of the catch per set over the corresponding estimated school size (calculated as the sum of the catch per set and the estimated escaped biomass). The observer's initial estimate of the estimated escaped biomass for successful sets was corrected following the procedure outlined in the Materials and methods section. The preliminary results indicated that the fraction of the school that escapes reached 17% for the small schools (estimated size lower than 20 t) and about 40% for the larger schools. These results suggest that catch per set frequency distribution overrepresents the small size structures (the class lower than 5 t reached 25% of the catch per set distribution, whereas the same class only represented 11% of the estimated school size distribution). An improvement in setting technology will modify not only the rate of unsuccessful sets but also the size of the catch per set (affecting total time in set, hence the amount of searching time and other variables related to the computation of an abundance index).

The differences between catch per set distribution and school size distribution are also due to the fact that fishers select tuna schools depending on different criteria. Since fishers do not record each real school size (such as observed before the decision to set the net), it is not possible to directly assess the school size distribution in the sea. However, it is possible to address this issue in an indirect way by using the proportion of successful sets ($P_i^+ = 1 - P_i^-$) and the proportion of schools chased and hauled (P_i^h) provided by

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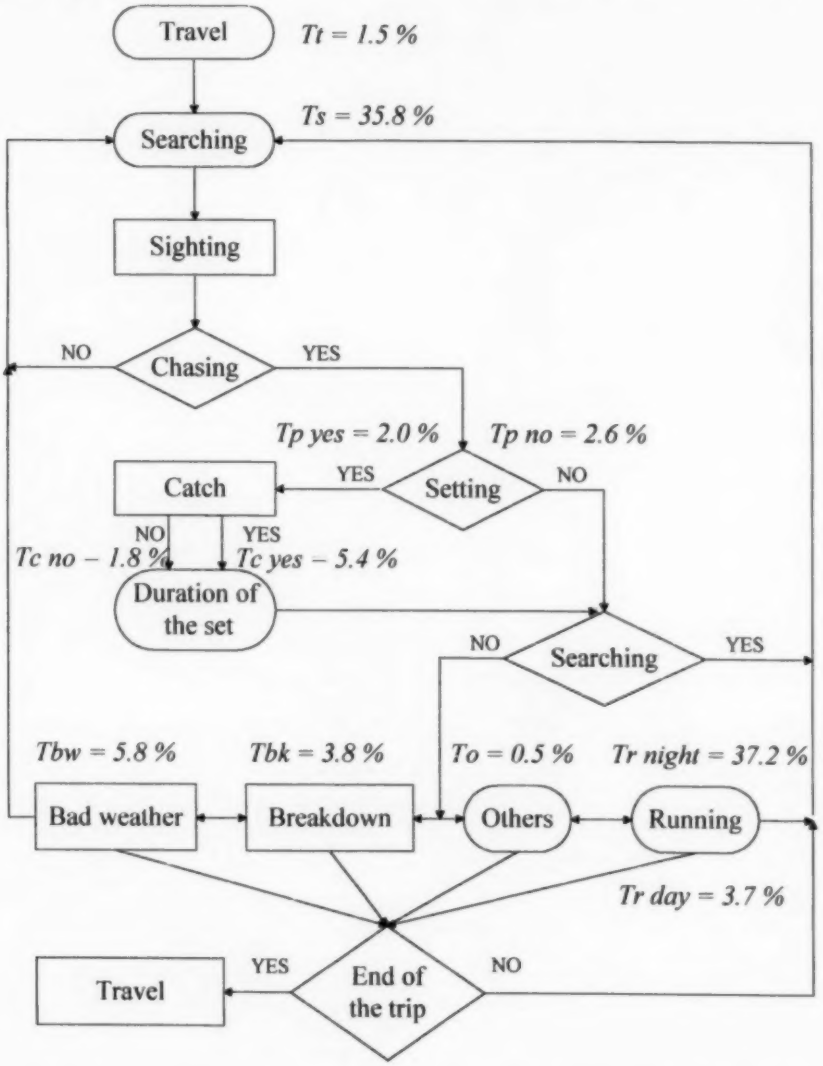
Fig. 6. Activity record of a purse seiner. Rectangles are events not depending on the skipper's behaviour and where duration cannot be cut down; rounded rectangles are activities or states; diamonds are fishers' decisions. Tt, percentage of time spent during travel activity (from port to fishing grounds); Ts, percent searching time; Tp yes, percent chasing time ended by a set; Tp no, percent chasing time not ended by a set; Tc yes, percent setting time for successful set; Tc no, percent setting time for unsuccessful set; Tbw, percent time of bad weather; Tbk, percent time during breakdown; To, percent time at other activities; Tr night, percent running time at night; Tr day, percent running time at day.



the logistic models. The total number of schools chased (but not automatically hauled and caught) (N_i^{ch}) is calculated as

$$N_i^{ch} = N_i^{+}/[(P_i^{+}) \cdot P_i^{h}]$$

where N_i^{+} is the observed number of successful sets for class size i.

It appeared that the proportion of schools smaller than 5 t reached 22% of the estimated school size distribution, whereas it represented only 11% of the total successful sets (Fig. 5). It was evident that the smallest schools were underrepresented in the catches and reciprocally that the larger ones were overrepresented. These discrepancies resulted from the differences in (*i*) successful rate and escapement and, for the major part, (*ii*) skippers' decisions. It is likely that changes in school size thresholds may introduce biases in the interpretation of any catch rate and abundance relationship.

Associations between tuna species or tuna size categories and sightings are well known by fishers. For instance, large yellowfin tuna are usually associated with dolphins in the eastern Pacific Ocean (Buckland and Anganuzzi 1988; Allen and Punsly 1984; Hall et al. 1992) or swim in nonassociated

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schools in others areas (e.g., eastern Atlantic Ocean, Ariz et al. 1992; Indian Ocean, Hallier and Parajua 1992; western Pacific Ocean, Hampton and Bailey 1992). In contrast, flotsam yields small fishes in all oceans. It is quite clear that the skipper's fine-scale decisions are influenced by the nature of the sighting. Another factor that can influence fishing success is the weather at sea. In poor sighting conditions (Beaufort > 4), a lower encounter rate can be anticipated (Buckland and Anganuzzi 1988). This value can also be considered as a threshold for the success of the fishing operations of a purse seiner (Fonteneau 1989). The present analysis confirmed that the weather at sea had a negative impact on the motivation to chase the school, apparently due to its interaction with the sightings (Fig. 3).

Conclusions

The analysis of purse-seiner fishers' behaviour has received little attention, although there are many aspects of skippers' decisions that influence the catchability of surface tuna schools. In the purse-seiner tuna fisheries, catch rates are defined as the quantity of fish caught in a set divided by the searching time preceding it (at least when the school is not associated with an artificial floating object equipped with a radio beacon). Searching time corresponds to the daylight hours spent on the fishing grounds minus (*i*) the time spent during unsuitable events (bad weather, etc.) and (*ii*) the time spent chasing and setting. Accordingly, good estimates of these amounta of time are necessary to obtain correct interpretation of the relationship between catch rates and abundance index.

This paper provides factorial evidence on how catchability can be affected by the interactions among fishers' fine-scale decisions, the fishing gear used, and some of the features of the school. In order to understand when these factors can influence the fishing process, a schematic daily activity record of a purse seiner was made showing the proportion of time spent in each type of activity (Fig. 6). The important results concerned the high percentage of time spent in the searching activity (35.8%) and the time spent in running at night (37.2%). The amount of time setting the net was estimated at 5.4% for positive sets (variable, positively related to the size of the catch) and at 1.8% for unsuccessful sets. Running means that the purse seiner was moving from one area to another, but not actively searching for signs of fish. However, bearing in mind the clustered distribution of tuna schools in space and time, running toward the concentrations should be included in the estimate of searching time (Laurec and Le Guen 1977). In the present study, it was evidenced that (*i*) moving locations occurred mainly at night and (*ii*) the amount of time spent chasing a school was approximately the same whether the net was set (2%) or not (2.6%). This fact reinforces some possible bias in the searching time estimates because in practice, it is difficult to evaluate the portion of running time devoted to the location of patches as well as the duration of the chasing (e.g., pursuits are not reported in logbooks). Given the lack of precise information of this type in logbooks as well as concerning the factors involved in different aspects of fishing behaviour, the use of at-sea observer data should be encouraged in order to periodically correct the logbook data.

The great amount of time spent searching within a fishing day could explain why major attempts to improve the vessel's searching capacity were made (use of bird radar for example). The other salient result concerns the amount of time spent setting the net. These data evidenced (*i*) why the opportunity cost associated with the decision to set the net is a considerable one for the skipper and (*ii*) why improvements in fishing gear are made in order to reduce the time taken to load the catch aboard, especially in the hauling power of purse winches and power blocks. As a general rule, considering that the cost of new equipment is low relative to the expected outcomes, fishers are encouraged to invest in fishing gear that can cut down these parts of a fishing day. Hence, conservative measures that determine the optimal level of fishing effort may take into account that tuna fishers are trying to reduce the time spent finding patches and hauling the net in order to limit either the overusage of new equipment or the number of fishing days per vessel.

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Natural and commercial dissolved organic matter protects against the physiological effects of a combined cadmium and copper exposure on rainbow trout (*Oncorhynchus mykiss*)

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Abstract: Environmentally realistic concentrations of a natural dissolved organic matter (DOM) (8 mg C/L as dissolved organic carbon (DOC)) protected against the acute respiratory and ionoregulatory effects of 0.2 μM Cd and 0.8 μM Cu on rainbow trout (*Oncorhynchus mykiss*). The protection afforded by low natural DOC was the same as that afforded by similar or higher concentrations of commercial DOC. Trout exposed to the metals alone experienced large decreases in arterial P_{O_2}, increases in arterial P_{CO_2}, increases in blood lactate, decreases in plasma concentrations of Cl, and developed pronounced haemoconcentration. There were no deleterious effects of 31 mg C/L commercial DOC on any measured aspect of trout physiology except for an increase in plasma Cl, which was probably due to elevated aqueous Cl concentrations associated with the DOM addition. No concentration of DOC used in the present study prevented Cd from being bound by trout gills, and some of these fish showed hypocalcemia; however, Cu was kept off the gills of trout exposed to metals plus DOM. Computer modelling using metal–gill binding constants simulated well the accumulation of Cd and the lack of Cu accumulation by trout gills in the presence of DOM.

Résumé : Des concentrations environnementales réalistes de matière organique dissoute (MOD) (concentration de carbone organique dissous (COD) de 8 mg C/L) ont assuré une protection contre les effets aigus sur la respiration et la régulation des ions de l'exposition à 0,2 μM de Cd et à 0,8 μM de Cu chez la truite arc-en-ciel (*Oncorhynchus mykiss*). La protection fournie par de faibles concentrations naturelles de COD était identique à celle fournie par des concentrations identiques ou supérieures de COD commercial. Les truites exposées aux seuls métaux ont montré une baisse importante de la P_{O_2} artérielle, un accroissement de la P_{CO_2} artérielle, un accroissement du lactate sanguin, une baisse des concentrations plasmatiques de Cl et une hémoconcentration prononcée. On n'a observé aucun effet néfaste de l'exposition à 31 mg C/L de COD commercial sur les paramètres physiologiques mesurés chez les truites, sauf un accroissement du Cl plasmatique probablement dû aux concentrations aqueuses de Cl élevées liées à l'addition de MOD. Aucune concentration de COD utilisée dans cette étude n'a empêché le Cd de se lier aux branchies des truites, et certains des poissons ainsi touchés ont souffert d'hypocalcémie; cependant, le Cu ne s'est pas lié aux branchies des poissons exposés aux métaux en même temps qu'à de la MOD. La modélisation informatique utilisant les constantes de liaison des métaux aux branchies a bien simulé l'accumulation de Cd et l'absence d'accumulation du Cu sur les branchies des truites en présence de MOD.

[Traduit par la Rédaction]

Introduction

Cadmium and Cu can have profound physiological effects on aquatic organisms and, like most other metals, have their greatest effects in soft water (Spry and Wiener 1991). This greater metal toxicity in soft water is reflected in models that consider the metal cation to be the most toxic form of a metal (Pagenkopf 1983; Rainbow et al. 1993). Waterborne metal cations can adhere to fish gills and cause toxic effects by interfering with ionoregulation, respiratory gas transfer, acid–base balance, and nitrogenous waste excretion (Wood 1992).

The toxic action of Cd at fish gills is through interactions with Ca uptake. Cadmium inhibits the basolateral Ca^{2+}-ATPase, thus inhibiting the influx of Ca across fish gills, leading to plasma hypocalcemia (Verbost et al. 1989; Wicklund Glynn et al. 1994). Copper causes toxicity in fish by interfering with Na and Cl regulation at the gills. Low concentrations of Cu impair Na and Cl influx at the gills by inhibiting basolateral Na^+,K^+-ATPase activity (Beckmann and Zaugg

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1988), leading to decreases in plasma Na and Cl concentrations, resulting in haemoconcentration and ultimately leading to cardiac failure (Wilson and Taylor 1993). Both metals have also been shown to impair respiratory gas transfer at fish gills (e.g., Majewski and Giles 1981; Wilson and Taylor 1993), and Cu has been shown to cause increases in plasma ammonia (Wilson and Taylor 1993) and increases in plasma cortisol (Pelgrom et al. 1995).

Dissolved organic matter (DOM) can reduce metal toxicity to aquatic organisms through chelation of metals to carboxyl and phenolic groups, reducing the amount of metal cation available for interactions with biological membranes (Erickson et al. 1996; Stumm and Morgan 1996). Once a metal is bound by DOM, the amount of metal binding to fish gills is determined by the relative binding strength of the metal to the DOM and the metal to the gills (e.g., Playle et al. 1993*a*, 1993*b*; Playle 1998; Richards and Playle 1998). DOM concentrations ≥4.8 mg C/L as dissolved organic carbon (DOC) prevented Cu binding to gills of fathead minnow (*Pimephales promelas*) exposed to 0.27 μM Cu for 3h, but ≥7.7 mg C/L DOC was needed to prevent Cd from binding to minnow gills in 3-h exposures to 0.05 μM Cd (Playle et al. 1993*a*). In longer exposures (7 and 15 days), DOM was shown to prevent Cu binding by rainbow trout (*Oncorhynchus mykiss*) gills but did not prevent Cd binding by trout gills (Hollis et al. 1996, 1997). In essence, Cu binds better to DOM than to fish gills and Cd binds better to fish gills than to DOM (Playle et al. 1993*b*).

Recently, DOM (as fulvic acids) has been shown to bind to isolated Atlantic salmon (*Salmo salar*) gill cells (Campbell et al. 1997) and to largemouth bass (*Micropterus salmoides*) gills (Wilkinson et al. 1993) at low aqueous pH. However, these studies did not indicate if these DOM–gill interactions had any deleterious effects on the fish. A high concentration of DOC (50 mg C/L DOC) has been shown to be nontoxic to trout (Goodrich et al. 1991), and 5 mg C/L DOC has been shown to have no effect on ventilation or oxygen consumption in Sacramento blackfish (*Orthodon microlepidotus*) (Chio et al. 1998). However, the possible respiratory and ionoregulatory effects of high concentrations of DOC have not been investigated.

The main objective of the present study was to examine the effects of natural and commercial DOM on the physiological effects of a combined Cd and Cu exposure on rainbow trout. A combined metal solution of Cd and Cu was used to simulate environmentally relevant exposures of fish to more than one metal at a time. The potential physiological effects of high concentrations of DOC in the absence of metals were also examined. Theoretical modelling using a modified aquatic equilibrium chemistry program, MINEQL$^+$, was done to determine if we could simulate Cd and Cu accumulation by the gills of trout exposed to metals in the absence and presence of added DOM.

Materials and methods

Experimental animals

Adult rainbow trout (~225 g) were purchased from Rainbow Springs Hatchery in Thamesford, Ont. Fish were held in 500-L tanks supplied with a continuous flow of dechlorinated Waterloo city tap water (8600 μM Na, 4500 μM Ca, pH 8.0, 15°C). Fish were fed every second day to satiation with trout pellets (Purina, New Hamburg, Ont.). One week before an experiment, 20 trout were acclimated to synthetic soft water in two 60-L polyethylene containers supplied with 100 mL soft water/min. Soft water was produced by a reverse osmosis system with an automatic conditioner (Culligan MP1000, series E reverse osmosis system, Culligan of Canada Ltd., Mississauga, Ont.). Chemistry of the acclimation water was 800 μM Na, 75 μM Ca, and pH 6.5. Fish were not fed during the acclimation period or during experiments.

Three separate metal plus DOM experiments were run, each with trout exposed to Cd and Cu in soft water with the addition of 20 mg C/L commercial DOC, 5 mg C/L natural DOC, or 5 mg C/L commercial DOC. The natural DOM was isolated by tangential flow ultrafiltration from Luther Marsh, near Grand Valley, Ont. (43°54′ N, 80°24′ W), as described in Hollis et al. (1996), and the commercial DOM was terrestrial (sodium salt, Sigma-Aldrich Chemical Company, St. Louis, Mo.). To assess the physiological effects of DOM itself, fish were exposed to metal-free soft water with and without the addition of 30 mg C/L commercial DOC.

Experimental protocols

Fish were anaesthetized with 0.08 g 3-aminobenzoic acid ethyl ester/L (methanesulfonate salt (MS 222), Sigma-Aldrich) buffered to pH 6.5 with KOH. Anaesthetized trout were fitted with dorsal aortic catheters using Clay-Adams PE-50 polyethylene tubing while their gills were irrigated with water containing anaesthetic (Soivio et al. 1972). A 30-cm length of PE-50 tubing was attached to each catheter with a needle connector and filled with heparinized Cortland saline (1.6 μg heparin/mL) (Wolf 1963). After surgery, trout were revived by irrigating their gills with soft water and each fish was placed into one of 13 dark, aerated, 2.5-L Plexiglas boxes supplied with 50 mL soft water/min (temperature 11.0°C) from a common head tank.

After 48 h of recovery from surgery, preexposure blood samples (P in figures) were taken from each fish. At time zero (vertical broken line in figures) the head tank and each box containing a fish were spiked with appropriate volumes of Cd, Cu, and DOM stock solutions to give nominal concentrations of 0.15 μM Cd and 0.75 μM Cu and various concentrations of DOM (see Table 1). The metal stock solution was delivered to the heavily aerated head tank by a peristaltic pump to maintain desired metal concentrations in each box. Flow from the head tank was split, and a concentrated stock solution of DOM was delivered by peristaltic pump into one half the flow (e.g., to either six or seven fish). Fish exposed to metals alone were run simultaneously with fish exposed to metals plus DOM, and treatments were interspersed to avoid position effects.

Arterial blood samples (1 mL) were drawn anaerobically into a chilled Hamilton gas-tight syringe before the start of each exposure and at 22, 46, 70, and 94 h thereafter. Smaller volumes of blood (500 μL) were drawn at 34 h for plasma ion analysis to reduce the total volume of whole blood removed from the fish. Sampled blood volume was replaced with Cortland saline (130 mM Cl, 140 mM Na, 1.6 mM Ca), and the catheter and extender were filled with heparinized Cortland saline. Blood samples were mixed to ensure homogeneity and were analyzed for arterial oxygen tension (P_{O_2}), arterial carbon dioxide tension (P_{CO_2}), pH, lactate, haematocrit (Ht), haemoglobin (Hb), and plasma concentrations of Cd, Cu, Na, Cl, Ca, and glucose, as described below. Ventilation rate of each fish and the number of coughs per minute were visually counted over 0.5 min.

Inspired water samples were taken at each sampling time and analyzed for aqueous P_{O_2}, P_{CO_2}, pH, and concentrations of Cd, Cu, Na, Cl, and Ca, as described below. Water for ion analysis was collected in 7-mL scintillation vials and acidified with two drops of ultrapure 16 N HNO_3. Samples for DOC analysis were collected in 7-mL combusted (450°C for 4 h) borosilicate vials without any

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Table 1. Chemical characteristics of exposure water from experiments with rainbow trout exposed to soft water containing metals and soft water containing metals plus DOM (measured as DOC).

	Metals plus high commercial DOC		Metals plus low natural DOC		Metals plus low commercial DOC	
	Metals	Metals plus DOM	Metals	Metals plus DOM	Metals	Metals plus DOM
Cd	0.15±0.01 (8)	0.18±0.01 (13) ns	0.19±0.01 (14)	0.18±0.01 (17) ns	0.35±0.01 (6)	0.34±0.01 (19) ns
Cu	0.74±0.03 (8)	0.82±0.02 (13) ns	0.73±0.04 (14)	0.80±0.02 (17) ns	0.58±0.01 (6)	0.59±0.02 (20) ns
DOC	2.5±0.1 (8)	21.8±1.3 (19)***	1.9±0.1 (21)	8.2±0.5 (17)***	2.0±0.1 (5)	6.6±0.1 (20)***
Ca	12±1 (18)	34±1 (28)**	10±2 (21)	18±3 (26)**	<2 (12)	10±5 (25) ns
Cl	250±20 (18)	1040±80 (27)***	260±11 (21)	320±10 (26)**	240±10 (12)	250±10 (25) ns
Na	500±40 (14)	750±30 (27)***	600±11 (21)	630±10 (26)*	540±10 (12)	510±10 (25) ns
pH	6.8±0.1 (10)	6.8±0.1 (20) ns	7.1±0.1 (21)	7.1±0.1 (26) ns	6.9±0.1 (12)	6.7±0.1 (25) ns
P_{O_2}	116±4 (10)	113±3 (20) ns	122±2 (21)	117±3 (26) ns	115±3 (12)	121±2 (25) ns
P_{CO_2}	1.1±0.1 (10)	1.1±0.1 (20) ns	1.0±0.1 (21)	1.1±0.1 (26) ns	1.1±0.1 (12)	1.0±0.1 (25) ns

Note: Cadmium, Cu, Ca, Cl, and Na concentrations are given in μM, DOC concentrations are given in mg C/L, and P_{O_2} and P_{CO_2} are given in torr, all as the mean ± 1 SEM (n). Temperature of all exposure water was 11.0 ± 0.1°C (n = 170). Differences between aqueous chemistry for metals-only exposure and metals plus DOM exposure from each experiment are indicated by asterisks: $^*P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$; ns, not significant.

head space, sealed with Teflon-lined caps, and stored refrigerated until analyzed (see below).

After 94 h, surviving trout from all treatments were stunned with a blow to the head and a section of gill lamellae from the second right gill arch was removed for determination of Cd and Cu concentrations. Each gill sample was rinsed for 10 s in 100 mL of deionized water to remove excess mucus and loosely bound Cd and Cu. Gill lamellae were digested in five times their wet weight of 1 N HNO_3 at 80°C for 3 h. Digest supernatant was diluted 10 times in deionized water and analyzed for total bound Cd and Cu using a graphite furnace atomic absorption spectrophotometer, as described below.

Analytical techniques

For each sample, arterial and inspired water P_{O_2} and P_{CO_2} and blood pH were measured at experimental temperature using Cameron microelectrodes (E101 O_2 electrode, E201 CO_2 electrode, E301 glass and E351 pH reference electrode) attached to a Cameron BGM200 blood gas meter (Cameron Instrument Company, Port Aransas, Tex.). Water pH was measured using a Radiometer PHM82 meter with GK2401C combination electrode.

Haematocrit was measured in duplicate using NH_4-heparinized microhaematocrit tubes (Fisher Scientific Ltd., Unionville, Ont.) centrifuged at 5900 × g for 5 min in a Clay-Adams centrifuge (model 0591, Fisher Scientific). Haemoglobin was measured colourimetrically on a 20-μL aliquot of whole blood using a cyanmethaemoglobin method (Sigma-Aldrich). Mean cell haemoglobin concentration was calculated by dividing Hb concentration by Ht and is reported as grams per decilitre. Whole blood lactate concentration was measured enzymatically (L,D-lactate dehydrogenase/NADH at 340 nm, Sigma-Aldrich) on blood that had been immediately deproteinized in two volumes of ice-cold 8% perchloric acid (Baker Analyzed Reagent, Phillipsburg, N.J.). Remaining blood was centrifuged at 12 700 × g for 2 min in a Micro MB centrifuge (model 3615, VWR Canlab, Mississauga, Ont.). Plasma supernatant from the centrifuge tubes and haematocrit tubes were combined and stored at –40°C.

Frozen plasma was thawed and diluted 750, 200, and 50 times in deionized water for analysis of Na, Cl, and Ca, respectively. Plasma and aqueous Na and Ca concentrations were determined on a Perkin Elmer model 3100 atomic absorption spectrophotometer; plasma and aqueous Ca samples were modified with 10% $LaCl_2$ (VWR Canlab) to reduce Na interference. Plasma and aqueous Cl concentrations were determined using a mercuric thiocyanate spectrophotometric method (Sigma-Aldrich). Plasma glucose concentrations were determined enzymatically (hexokinase, glucose-6-phosphate dehydrogenase, Sigma-Aldrich). Plasma was also diluted 10 times in 0.1 N HNO_3 for analysis of Cd and Cu concentrations.

Plasma, water, and gill Cd and Cu concentrations were measured using a graphite furnace atomic absorption spectrophotometer (Varian AA-600 with GTA-100 atomizer) with 10-μL injections and argon gas. Cadmium operating conditions were those given by Varian except for shorter drying times and were 5 s drying time at 85°C, 30 s at 95°C, 10 s at 120°C, and 4.8 s at 1800°C, during which Cd was measured against standards prepared from a certified standard (1000 mg Cd/L, Fisher Scientific). Copper operating conditions were those given by Varian except for shorter drying times and were 5 s drying time at 85°C, 30 s at 95°C, 10 s at 120°C, 8 s at 800°C, and 5.1 s at 2300°C, during which Cu was measured against standards prepared from a certified standard (1000 mg Cu/L, Fisher Scientific). Half the aqueous DOM samples were analyzed on a Beckmann model 915B total carbon analyzer, after acidification and sparging to remove inorganic carbon, and are reported as DOC in milligrams of C per litre. A standard curve of absorbance at 340 nm was created from these measured DOC concentrations, and DOC concentrations of the remaining samples were determined by their absorbance at 340 nm.

Data presentation

Experimental data are presented as means ± 1 SEM (n). Statistical analysis consisted of a one-way analysis of variance followed by a Student–Newman–Keuls method or Dunn's method of pairwise multiple comparisons, whichever was appropriate, to evaluate differences compared with preexposure values (P in figures).

Results

Mortality

One hundred percent mortality was observed in cannulated rainbow trout exposed to Cd and Cu in soft water in the absence of added DOM. Mortality in trout exposed to the two metals occurred within 48 h after the start of exposure, except for one fish that survived to 70 h (Figs. 1–4). The addition of high and low concentrations of commercial DOC to soft water containing metals generally prevented metal-induced toxicity, although some mortality was observed in trout exposed to metals plus low natural DOC. In the metals plus low natural DOC exposure, one trout died before 70 h and two more trout died before the 94-h sampling time (see Fig. 1D; see Table 1 for aqueous chemistry). No mortalities were observed in trout exposed to metal-free

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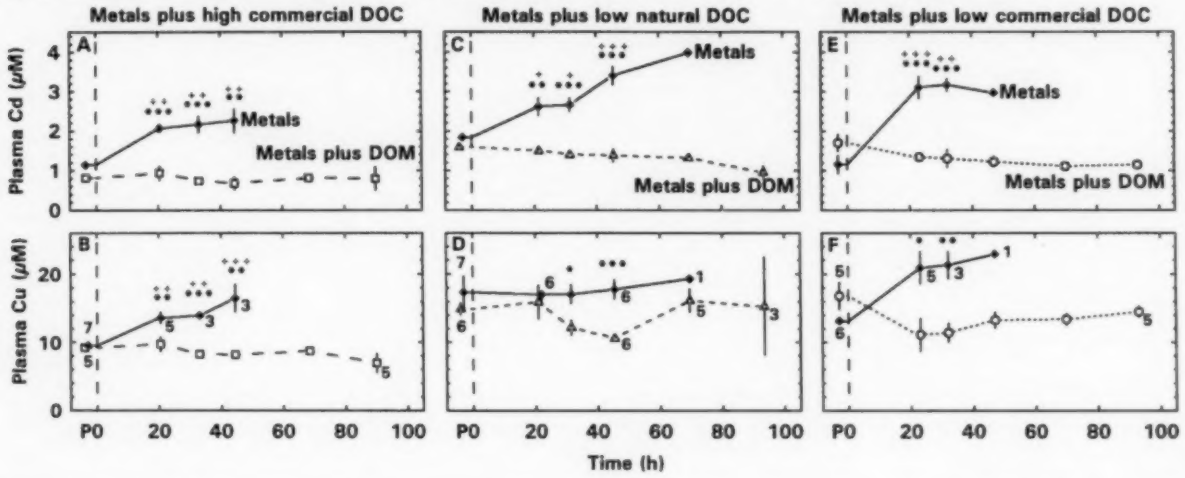
Fig. 1. Accumulation of Cd and Cu in plasma of rainbow trout exposed to Cd and Cu in the absence (solid lines) or presence (broken lines) of DOM. Each point represents the mean ± 1 SEM during the preexposure sample (P) and following 22, 34, 46, 70, and 94 h of exposure to metals alone and metals plus DOM. Symbols are offset for clarity where necessary. Numbers on Figs. 1B, 1D, and 1F refer to the number of fish for each sampling time for each treatment if there was a change from the previous sampling time. Asterisks represent significant differences between the two exposure groups (*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$), and crosses represent significant differences compared with the preexposure sample (+, $P < 0.05$; ++, $P < 0.01$; +++, $P < 0.001$).



water or to metal-free water plus high commercial DOC (Fig. 5; see Table 2 for aqueous chemistry).

Plasma Cd and Cu accumulation

Trout exposed to metals alone showed two to three times increases in plasma Cd and Cu concentrations (Figs. 1A, 1B, 1E, and 1F). The addition of high and low concentrations of commercial DOC prevented the entry of Cd and Cu into trout plasma. Similarly, low concentrations of natural DOC prevented Cd accumulation in trout plasma even during the last 24-h exposure when trout were accidentally exposed to elevated aqueous metal concentrations (0.25 ± 0.02 μM Cd (n = 3) and 1.98 ± 0.2 μM Cu (n = 3) (Fig. 1C). Trout exposed to metals plus low natural DOC had lower plasma Cu concentrations at 34 and 46 h compared with trout exposed to metals alone (Fig. 1D).

Respiratory effects

Trout exposed to metals alone experienced decreases in arterial P_{O_2} (Figs. 2A, 2E, and 2I) and increases in arterial P_{CO_2} (Figs. 2B, 2F, and 2J) compared with preexposure samples. These effects of Cd and Cu on respiratory gas transfer were prevented by the addition of low and high concentrations of commercial DOC and low concentrations of natural DOC (Fig. 2).

Ventilation rates of trout were not affected by exposure to metals alone or to metals plus low natural or commercial DOC (Table 3); however, trout exposed to metals alone showed increased ventilation volumes compared with trout exposed to metals plus DOM. The number of rapid opercular movements ("coughs") increased upon metal exposure, but the addition of low natural or commercial DOC to water containing metals prevented the increase in cough rate. Ventilation and cough rates were not counted in the metals plus high commercial DOC experiment because the fish were not visible in the dark-brown DOM-supplemented water.

The addition of high concentrations of commercial DOC and low concentrations of commercial and natural DOC prevented the large increases in blood lactate concentrations observed in trout exposed to metals alone (Figs. 2C, 2G, and 2K). In the trout exposed to the metals plus low natural DOC, there were low but significant increases in blood lactate at 94 h (Fig. 2G). An extracellular acidosis was observed in trout exposed to metals alone from the metals plus high commercial DOC experiment (Fig. 2D), but no other significant decreases in arterial pH were observed in trout exposed to metals alone or to metals plus DOM (Figs. 2H and 2L).

Ionoregulatory effects

Plasma Cl concentrations decreased in trout exposed to metals alone compared with trout exposed to metals plus high commercial DOC and low natural DOC (Figs. 3A and 3C). There were no effects of metal exposure on plasma Cl concentrations from the metals plus low commercial DOC experiment (Fig. 3E). Slight, but not significant decreases in plasma Na concentrations were observed in trout exposed to metals alone compared with trout exposed to metals plus DOM (Figs. 3B, 3D, and 3F).

No changes in plasma Ca concentrations were observed in trout exposed to metals alone or to metals plus high or low commercial DOC (Figs. 4A and 4E). In contrast, trout exposed to metals alone from the low natural DOC experiment showed a slight, initial decrease in plasma Ca concentrations followed by an increase at ≥46 h of exposure; conversely, plasma Ca concentrations in trout exposed to metals plus low natural DOC decreased continuously over the 94-h exposure (Fig. 4C).

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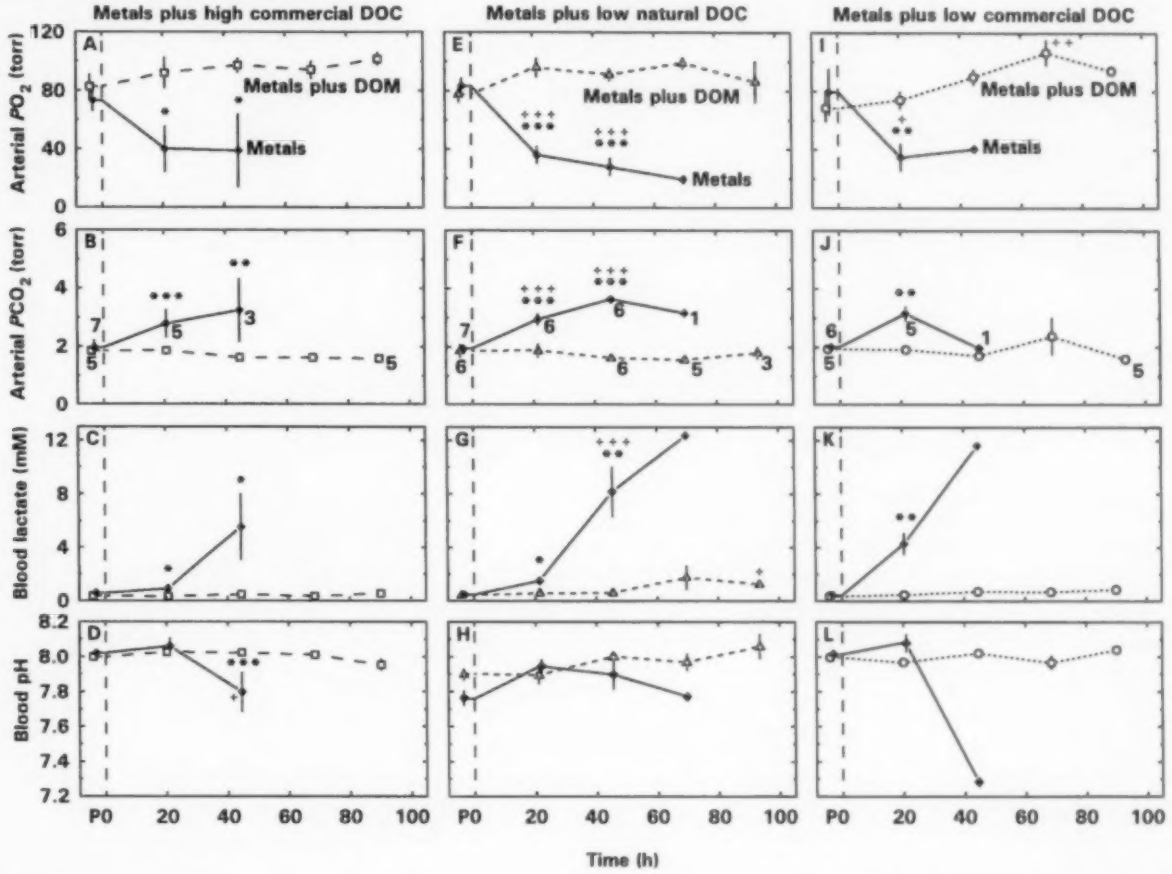
Fig. 2. Arterial O_2 tension, arterial CO_2 tension, blood lactate concentrations, and arterial pH from rainbow trout exposed to Cd and Cu in the absence (solid lines) or presence (broken lines) of DOM. Each point represents the mean ± 1 SEM during the preexposure sample (P) and following 22, 46, 70, and 94 h of exposure to metals alone and metals plus DOM. Numbers on Figs. 2B, 2F, and 2J refer to the number of fish for each sampling time for each treatment if there was a change from the previous sampling time. See caption to Fig. 1 for further details.



Haematological effects

Mean cell Hb concentrations (MCHC) decreased significantly in trout exposed to metals alone compared with constant MCHC in trout exposed to metals plus DOM (Figs. 4B, 4D, and 4F). The decreases in MCHC of trout exposed to metals alone were due to small changes in blood Hb (decrease) and blood Ht (increase), although neither parameter differed significantly when considered alone. In contrast, trout exposed to metals plus DOM had significant decreases in both Hb and Ht. Mean blood Hb and Ht were not statistically different within treatments at each sampling time; therefore, means are reported for all fish exposed to metals alone and all fish exposed to metals plus DOM. In trout exposed to metals alone, blood Hb did not vary significantly and was 7.3 ± 0.6 g/dL (n = 18) at the preexposure sample, 7.6 ± 0.6 g/dL (n = 17) at 22 h, 7.4 ± 0.8 g/dL (n = 7) at 46 h, and 9.7 g/dL (n = 1) at 70 h. Blood Ht increased nonsignificantly in trout exposed to metals alone from 25.4 ± 1.8% (n = 19) at the preexposure sample to 27.4 ± 2.2% (n = 17) at 22 h, to 31.2 ± 4.1% (n = 7) at 46 h, and to 46.8% (n = 1) at 70 h. Blood Hb decreased significantly in trout exposed to metals plus DOM from 6.6 ± 0.6 g/dL (n = 16) at the preexposure sample to 2.4 ± 0.3 g/dL (n = 13) at 94 h of exposure ($P < 0.001$). Blood Ht decreased significantly in trout exposed to metals plus DOM from 22.4 ± 2.1% (n = 16) at the preexposure sample to 8.6 ± 1.0% (n = 13) at 94 h of exposure ($P < 0.001$).

Plasma glucose concentrations remained constant in all trout exposed to metals alone and to metals plus DOM and were 8.6 ± 0.6 mM (n = 60) and 5.7 ± 0.4 mM (n = 92), respectively. Plasma glucose concentrations were significantly higher ($P < 0.05$) in trout exposed to metals alone compared with trout exposed to metals plus low commercial DOM at 22 h (9.1 ± 1.6 mM (n = 4) and 4.0 ± 1.1 mM (n = 5), respectively); otherwise, there were no significant differences between exposures within an experiment.

Metal-free experiments

To assess the effects of DOM and repetitive blood sampling on trout physiology, cannulated trout were exposed to

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Fig. 3. Plasma Cl and Na concentrations from rainbow trout exposed to Cd and Cu in the absence (solid lines) or presence (broken lines) of DOM. Note the different vertical scale on Fig. 3E on the right. Each point represents the mean ± 1 SEM during the preexposure sample (P) and following 22, 34, 46, 70, and 94 h of exposure to metals alone and metals plus DOM. Numbers on Figs. 3B, 3D, and 3F refer to the number of fish for each time for each treatment if there was a change from the previous sampling time. See caption to Fig. 1 for further details.

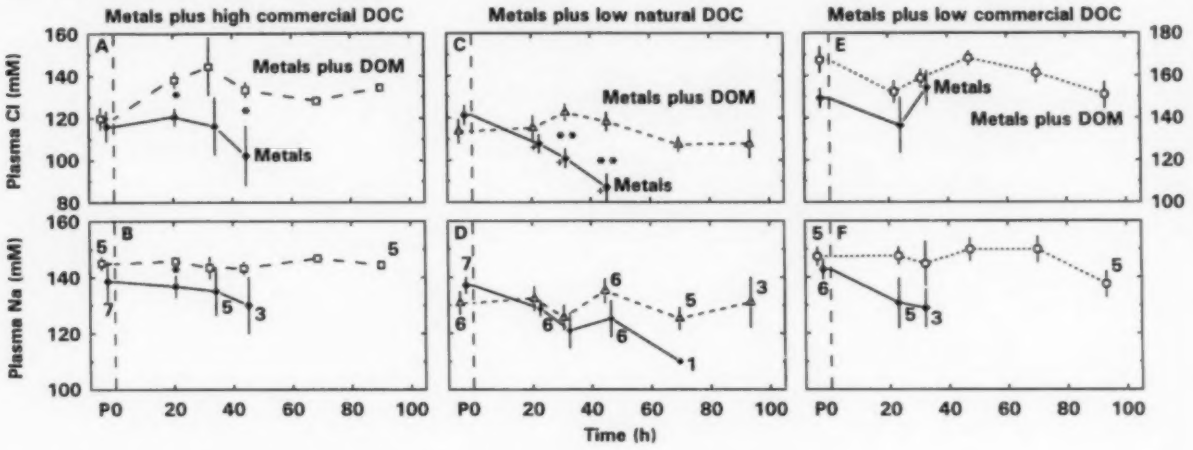
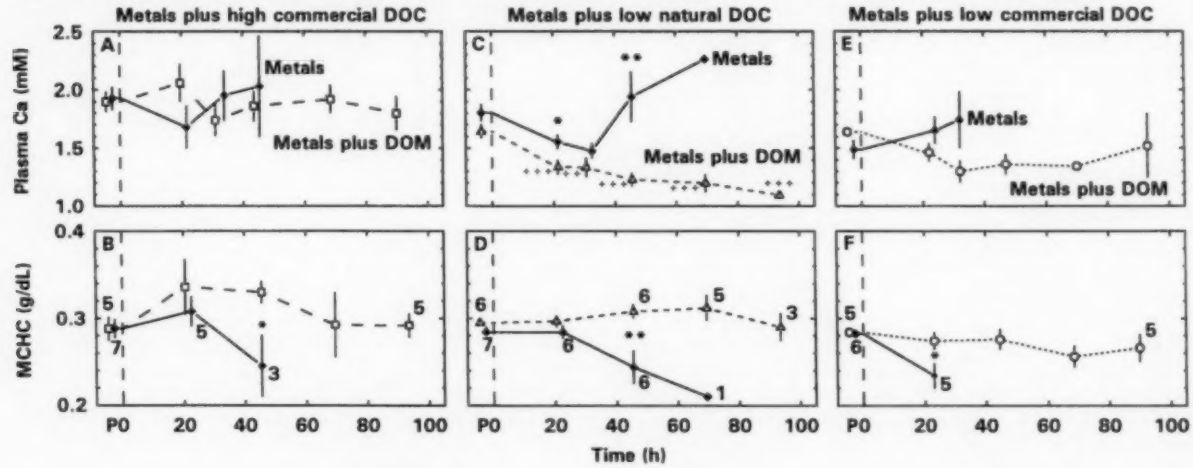


Fig. 4. Plasma Ca and mean cellular Hb concentrations (MCHC) from rainbow trout exposed to Cd and Cu in the absence (solid lines) or presence (broken lines) of DOM. Each point represents the mean ± 1 SEM during the preexposure sample (P) and following 22, 34, 46, 70, and 94 h of exposure to metals alone and metals plus DOM. Numbers on Figs. 4B, 4D, and 4F refer to the number of fish for each time for each treatment if there was a change from the previous sampling time. See caption to Fig. 1 for further details.



metal-free water and to metal-free water plus high commercial DOC (see Table 2 for aqueous chemistry). Plasma Cd and Cu concentrations did not increase in these trout: mean plasma Cd concentrations in trout exposed to metal-free water and to metal-free water plus high commercial DOC were 0.6 ± 0.1 μM Cd (n = 24) and 0.7 ± 0.1 μM Cd (n = 34), respectively. Mean plasma Cu concentrations in trout exposed to metal-free water and to metal-free water plus high commercial DOC were 11.7 ± 1.7 μM Cu (n = 24) and 10.6 ± 0.4 μM Cu (n = 34), respectively.

Trout exposed to either metal-free water or metal-free water plus high commercial DOC did not experience any impairment of respiratory gas transfer; arterial P_{O_2} remained constant at preexposure values for the duration of the experiment (Fig. 5A). In trout exposed to metal-free water, arterial P_{CO_2} remained constant at 2.1 ± 0.1 torr (1 torr = 133.322 Pa) (n = 20) over 90 h of exposure, and in trout exposed to metal-free water plus high commercial DOC, arterial P_{CO_2} decreased significantly from 2.2 ± 0.2 torr (n = 5) at the preexposure value to 1.7 ± 0.1 torr (n = 6) at 90 h (P < 0.05). Ventilation rates were not taken in these experiments because trout exposed to high commercial DOC were not visible in their boxes.

Blood lactate concentrations remained low and constant in trout exposed to metal-free water and to metal-free water plus high commercial DOC (Fig. 5B). Initial blood pH of the

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Table 2. Chemical characteristics of metal-free water and metal-free water supplemented with commercial DOC.

	Metal free	Metal free plus DOM
Cd	<0.001 (7)	0.05±0.01 (24) ns
Cu	0.09±0.03 (7)	0.13±0.01 (24) ns
DOC	2.4±0.1 (10)	31.1±1.6 (27)***
Ca	50±10 (20)	120±20 (30)*
Cl	300±30 (20)	1600±120 (30)***
Na	640±60 (20)	1020±40 (30)***
pH	6.9±0.1 (20)	7.1±0.1 (30) ns
P_{O_2}	119±3 (20)	114±2 (30) ns
P_{CO_2}	1.1±0.1 (20)	1.0±0.1 (30) ns

Note: Cadmium, Cu, Ca, Cl, and Na concentrations are given in μM, DOC concentrations are given in mg C/L, and P_{O_2} and P_{CO_2} are given in torr, all as the mean ± 1 SEM (n). See caption to Table 1 for further details.

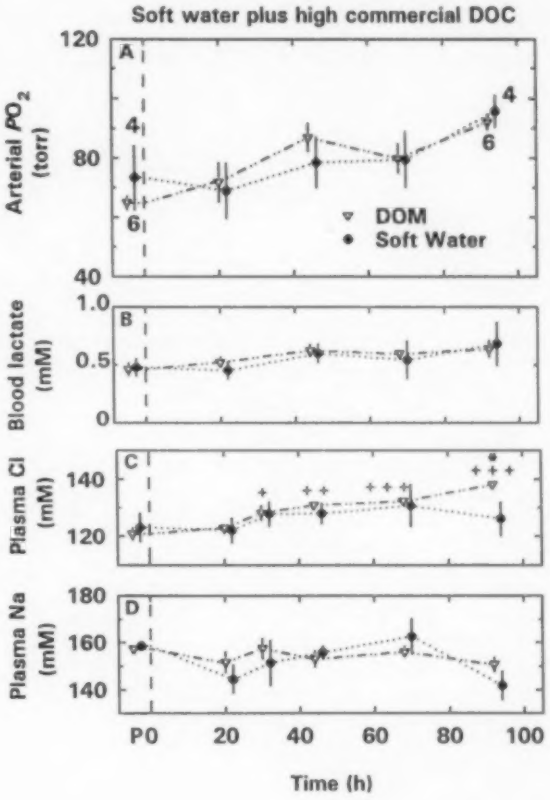
two groups of trout was significantly different ($P < 0.05$) at pH 7.95 ± 0.02 ($n = 6$, metal-free water) and 7.86 ± 0.02 ($n = 4$, metal-free water plus high commercial DOC). Blood pH remained significantly different until 69 h after the start of exposure when blood pH of the two groups converged at pH 8.0 and remained statistically equal to the end of the experiment.

Plasma Cl concentrations increased in trout exposed to metal-free water plus high commercial DOC compared with preexposure samples, but plasma Cl remained constant in trout exposed to metal-free water (Fig. 5C). Plasma Na concentrations remained constant at preexposure values in trout exposed to both metal-free water and to metal-free water plus high commercial DOC (Fig. 5D). Plasma Ca concentrations were unaffected by repetitive blood sampling or by the addition of high commercial DOC: mean plasma Ca concentration was 2.0 ± 0.1 μM Ca in each exposure ($n = 21$ or 31).

There were no differences in whole-blood measurements between trout exposed to metal-free water or to metal-free water plus high commercial DOC. MCHC's remained near preexposure values in trout exposed to metal-free water or to metal-free water plus high commercial DOC at 0.30 ± 0.01 g/dL ($n = 30$) and 0.29 ± 0.01 g/dL ($n = 20$), respectively. Blood Hb and Ht decreased steadily over the duration of the experiment, due to repetitive blood sampling. Blood Hb decreased from 6.4 ± 0.3 g/dL ($n = 4$) at the preexposure sample to 2.4 ± 0.4 g/dL ($n = 4$) at 90 h of exposure to metal-free water ($P < 0.001$) and from 7.9 ± 0.4 g/dL ($n = 6$) at the initial sample to 3.2 ± 0.4 g/dL ($n = 6$) at 90 h of exposure to metal-free water plus high commercial DOC ($P < 0.001$). Blood Ht decreased in trout from 22.0 ± 1.1% ($n = 4$) at the preexposure sample to 8.5 ± 1.5% ($n = 4$) at 90 h of exposure to metal-free water ($P < 0.001$) and decreased from 27.2 ± 1.6% ($n = 6$) at the preexposure sample to 10.4 ± 0.8% ($n = 6$) at 90 h of exposure to metal-free water plus high commercial DOC ($P < 0.001$).

Plasma glucose decreased in trout exposed to metal-free water from 0.6 ± 0.1 mM ($n = 4$) at the preexposure sample to 0.3 ± 0.1 mM ($n = 4$) at 90 h of exposure ($P < 0.01$). Plasma glucose remained constant at 0.4 ± 0.1 mM ($n = 30$) in trout exposed to metal-free water plus high commercial DOC.

Fig. 5. Arterial O_2 tension, blood lactate concentration, and plasma Cl and Na concentrations from rainbow trout exposed to metal-free water (dotted line, $n = 4$ throughout) and to metal-free water plus high commercial DOC (dashed–dotted line, $n = 6$ throughout). Each point represents the mean ± 1 SEM during the preexposure sample (P) and following 20, 35, 48, 68, and 96 h of exposure to metal-free water and metal free water plus high commercial DOC. See caption to Fig. 1 for further details.



Gill metal concentrations

Cadmium was accumulated by the gills of trout exposed to metals plus DOM compared with trout exposed to metal-free water (Fig. 6A). Copper was not accumulated by the gills of trout exposed to metals plus DOM compared with trout exposed to metal-free water, although it appeared that the addition of high commercial DOC kept Cu off trout gills better than lower concentrations of commercial or natural DOC (Fig. 6B). No gill Cd or Cd data were available for trout exposed to metals alone because all trout died before 94 h, when gill samples were taken.

Modelling Cd and Cu speciation and binding to trout gills

To model the effects of DOM on Cd and Cu speciation and binding to trout gills, we modified a chemical equilibrium program, MINEQL$^+$ (Schecher and McAvoy 1992), to include conditional equilibrium binding constants for Cd,

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Table 3. Ventilation rate (VR) and cough rate (CR) of rainbow trout exposed to metals only and metals plus low natural and commercial DOC.

	Metals plus low natural DOC				Metals plus low commercial DOC			
	Metals		Metals plus DOC		Metals		Metals plus DOC	
Time (h)	VR	CR	VR	CR	VR	CR	VR	CR
Preexposure	59±4 (7)	<1 (7)	56±5 (6)	<1 (6)	78±8 (5)	<1 (5)	57±4 (5)	<1
22	79±5 (7) ns	14±2 (7)*	66±3 (6) ns	<1 (6) ns	82±8 (4) ns	11±3 (4)***	63±5 (5) ns	<1 ns
46	64±9 (6) ns	7±3 (5)*	67±5 (6) ns	<1 (6) ns	—	—	73±6 (5) ns	<1 ns
70	60 (1) ns	<1 (1) ns	68±6 (5) ns	2±1 (5) ns	—	—	68±6 (5) ns	<1 ns
94	—	—	81±9 (2) ns	<1 ns	—	—	82±8 (5) ns	<1 ns

Note: VR and CR are reported per minute. VR and CR were not measured in trout exposed to metals plus high commercial DOC or to metal-free water plus high commercial DOC because the fish were not visible in the boxes due to the dark colour of the water. See caption to Table 1 for further details.

Cu, and H ion interactions at sites on DOM and Cd, Cu, Ca, and H ion interactions at the gills (Table 4) (Playle et al. 1993*b*; Hollis et al. 1997). The number of binding sites on DOC was 100 nmol binding sites/mg C, the value from Hollis et al. (1997).

The number of Cd and Cu binding sites at trout gills was estimated from Fig. 6 to be ~20 nmol Cd/g wet tissue and ~50 nmol Cu/g wet tissue. A molar concentration of gill Cd and Cu binding sites for use in the MINEQL$^+$ modelling was calculated in the following manner (see Richards and Playle 1998). Each adult trout had ~3 g of gill filament tissue; therefore, using 20 nmol Cd binding sites/g wet gill tissue and 50 nmol Cu binding sites/g wet gill tissue, there were about 60 nmol Cd binding sites/fish and 150 nmol Cu binding sites/fish. Each fish in its box was in 2.5 L of water; therefore, there were a total of 24 nM Cd binding sites/exposure chamber and 60 nM Cu binding sites/exposure chamber. Sensitivity modelling indicated that even twofold increases or decreases in the small number of estimated Cd and Cu binding sites on trout gills made only minor differences in the partitioning of Cd and Cu in the model. Modelling results using the modified MINEQL$^+$ computer program and measured water chemistry (Table 1) are given in Table 5.

The modelling exercise indicated that DOM readily keeps Cu off trout gills but does not keep Cd off trout gills (Table 5), which was indicated by the gill metal concentrations given in Fig. 6. We also modelled the effects of increases in aqueous Na, Cl, and Ca concentrations that accompanied the addition of DOM to separate the protective effects of DOM from the protective effects of increased aqueous ions (Table 1). That is, we considered changes in ion concentrations due to the addition of DOM while leaving aqueous DOC at background concentrations.

These simulations indicated that DOM was the major parameter in protecting against the effects of Cd and Cu on trout in our experiments and that increases in aqueous ion concentrations had only small effects on Cd speciation and inconsequential effects on Cu speciation. For example, taking the largest increases in water ions (metals plus high commercial DOC experiment) and leaving DOC at background concentrations only reduced cationic Cd concentrations to 78% (from 83%), reduced the amount of Cd bound by gills to 91% (from 95%), and had no effect (<1%) on Cu speciation compared with the absence of added ions (cf. Table 5). Conversely, adding DOM but leaving ion concentrations at background levels reduced the cationic Cd concentration to 3%, reduced the Cd bound by gills to 36%, reduced the cationic Cu concentrations to <1%, and reduced the Cu bound by gills to 1% (cf. Table 5). Therefore, DOM was the major factor protecting against the physiological and toxicological effects of Cd and Cu on trout.

Discussion

The present study demonstrated that DOM protects against the acute physiological effects of Cd and Cu exposure on rainbow trout while having no deleterious effects of its own, even at high concentrations. Both high and low concentrations of commercial DOC, and environmentally relevant low concentrations of natural DOC, completely protected against metal accumulation in trout plasma and prevented most metal-induced physiological changes in trout. However, no concentration of DOC used in the present study prevented Cd from being bound by trout gills, and some fish showed plasma hypocalcemia. Copper was kept off the gills of trout exposed to Cd and Cu in the presence of DOM. Modelling using a modified MINEQL$^+$ computer program and metal–gill conditional equilibrium stability constants simulated well the accumulation of Cd by trout gills and the lack of Cu accumulation by trout gills in the presence of DOM.

In general, trout exposed to Cd and Cu alone accumulated four to six times more Cd in the plasma and six to 15 times more Cu in the plasma compared with Cd and Cu concentrations in the water (cf. Fig. 1 and Table 1). These high concentrations of Cd and Cu observed in trout plasma compared with the surrounding environment suggest that Cd and Cu were bound by trout gills and then transported across the gill epithelium into plasma, possibly by accidental incorporation into active transport pumps (Rainbow et al. 1993; Heath 1995). Cadmium and Cu uptake at trout gills may also have been due to passive transport of Cd and Cu along increasing affinity binding sites across the gill epithelium (Rainbow et al. 1993). The uptake of Cd and Cu at the trout gill epithelium was likely facilitated by high calculated concentrations of Cd and Cu cations present in soft water without added DOM, as indicated by metal speciation calculations (Table 5).

We were not able to assess the binding of Cd and Cu by the gills of trout exposed to metals alone because all those fish died by 94 h. However, previous studies in our laboratory demonstrated that juvenile rainbow trout exposed to Cd

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Table 4. Data used to modify the MINEQL+ computer program to predict the speciation and partitioning of Cd and Cu in the absence or addition of DOM.

Complex	log *K*	Number of binding sites
Cd – gill Cd	8.6	Gill Cd = 20 nmol/g wet tissue
Ca – gill Cd	5.0	= 24 nM binding sites
H – gill Cd	6.7	
Cu – gill Cu	7.4	Gill Cu = 50 nmol/g wet tissue
Ca – gill Cu	3.4	= 60 nM binding sites
H – gill Cu	5.4	
Cd–DOM	7.4	DOM = 100 nmol binding sites/mg C
Cu–DOM	9.1	
H–DOM	4.0	

Note: Gill conditional equilibrium binding constants (log *K*) are from Playle et al. (1993*b*) and the number of binding sites on DOM was taken from Hollis et al. (1997). The numbers of Cd and Cu binding sites on rainbow trout gills were estimated from Fig. 6 and were converted to molar concentrations for use in the MINEQL+ program. See text for further details.

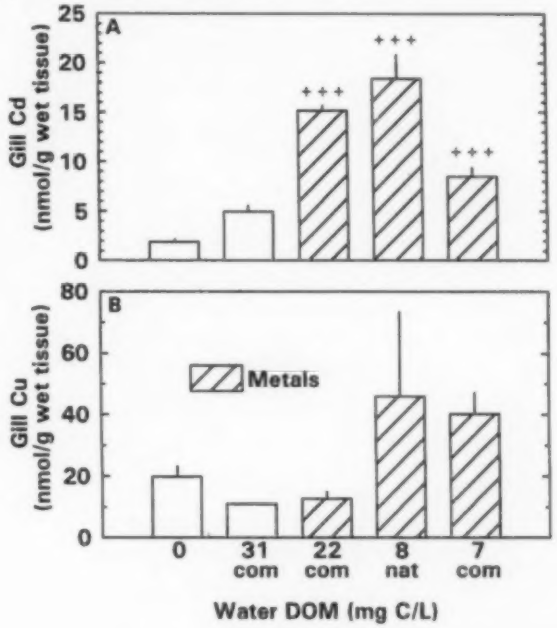
and Cu under similar conditions to those used in the present study accumulated high concentrations of Cd and Cu at their gills in short 2- to 4-h exposures (Hollis et al. 1996, 1997), and saturation of the gill Cd and Cu sites occurred in 1–2 days (Hollis et al. 1997). In the present study, it was reasonable to assume that the gills of trout exposed to metals alone were saturated with Cd and Cu before death occurred at ~2 days. This assumption agrees well with theoretical modelling, which suggested that the metal binding sites of the gills of trout exposed to metals alone were 95–98% saturated with Cd and 70–86% saturated with Cu (Table 5).

The complex suite of respiratory and ionoregulatory responses observed in trout exposed to metals alone was likely due to Cd and Cu cations interacting at the gill epithelium. Metal binding to fish gills can cause irritation and damage to the gill and increase the water–blood diffusion distance (McDonald and Wood 1993; Heath 1995). Increased diffusion distance, coupled with increased mucus production (Heath 1995), was probably responsible for the measured internal hypoxemia (Figs. 2A, 2E, and 2I) and hypercapnia (Figs. 2B, 2F, and 2J) in trout exposed to metals alone. Both metals have been shown to disrupt respiratory gas transfer at fish gills through metal-induced gill damage and excess mucus production (e.g., Majewski and Giles 1981; Wilson and Taylor 1993). In an attempt to compensate for their internal hypoxemia, trout exposed to metals alone increased the volume of water passing over their gills as judged qualitatively, and the increased number of coughs (Table 3) was probably an attempt to rid the gills of mucus buildup and restore oxygen fluxes across the gill.

Accompanying impaired oxygen flux at the gills of trout exposed to metals alone were large increases in blood lactate concentrations from anaerobic glycolysis (Figs. 2C, 2G, and 2K). The increases in blood lactate, coupled with internal hypercapnia, caused a combined metabolic and respiratory extracellular acidosis in two of the three experiments (Figs. 2D, 2H, and 2L). Wilson and Taylor (1993) also noted an increase in blood lactate and an extracellular acidosis in rainbow trout exposed to 4.9 μM Cu.

Copper has been shown to inhibit Na and Cl influx at low Cu concentrations and stimulate Na and Cl efflux at higher

Fig. 6. Terminal gill Cd and Cu concentrations from rainbow trout exposed to metal-free water with and without added DOM (open bars) and to Cd and Cu in the presence of commercial and natural DOM (hatched bars). From left to right, gill samples were taken from trout exposed for 94 h to metal-free water (n = 4), metal-free water plus high commercial DOC (n = 6), metals plus high commercial DOC (n = 5), metals plus low natural DOC (n = 3), and metals plus low commercial DOC (n = 5). Crosses represent significant differences compared with gills from fish in the metal-free water with or without added DOM (open bars) (+++, $P < 0.001$).



Cu concentrations (Laurén and McDonald 1985; Reid and McDonald 1988). In the present study, trout exposed to metals alone generally had reduced plasma Na and Cl concentrations (Fig. 3). The observed decreases in plasma Na and Cl were probably due to competitive inhibition by Cu and Cd of Na and Cl influx at trout gills and possible stimulation of Na and Cl efflux (Reid and McDonald 1988). The decrease in plasma Na and Cl concentrations in trout exposed to metals alone resulted in a reduction in the osmotic potential of the extracellular fluid and a shift of water from the extracellular space into the intracellular compartment. The consequence was a decline in plasma volume and haemoconcentration in these fish, as indicated by decreases in MCHC (Figs. 4B, 4D, and 4F). Reduced plasma volume was probably responsible for the observed increase in plasma Ca concentrations in trout exposed to metals alone (Fig. 4C, also see Fig. 4E).

The observed disruption in ionoregulatory mechanisms and the resulting osmotic imbalance are similar to responses observed in trout exposed to Cu (Wilson and Taylor 1993) and low pH (Milligan and Wood 1982) and recently observed for ionic Ag (Wood et al. 1996). It was concluded that the cause of death in trout exposed to Cu, low pH, and Ag was cardiac failure due to increased blood viscosity. In

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Table 5. Theoretical chemical speciation of Cd and Cu in the absence or addition of DOM as simulated by a modified MINEQL⁺ computer program (see Table 4).

	Percentage speciation					
	22 mg C/L commercial DOM		8 mg C/L natural DOM		7 mg C/L commercial DOM	
Complex	Metals only	Metals plus DOM	Metals only	Metals plus DOM	Metals only	Metals plus DOM
Cd^{2+}	83	3	82	44	89	60
Cd–DOM	2	93	3	42	2	31
Cd–gill	13 (95)	4 (28)	12 (96)	12 (91)	7 (98)	7 (97)
Cu^{2+}	32	<1	13	2	31	4
Cu–DOM	30	100	25	88	33	90
Cu–gill	7 (86)	<1 (1)	6 (70)	2 (26)	8 (81)	3 (33)
$Cu(OH)_{2\ (aq)}$	28	<1	51	7	24	3

Note: Indicated are percentages of the total concentration of Cd and Cu present in our experimental water as the cationic metal, metal bound by DOM, and metal bound by rainbow trout gills. The percentage of gill sites occupied by Cd and Cu is given in parentheses. The $Cu(OH)_{2\ (aq)}$ complex is given, but other more minor Cd and Cu complexes have been left out for clarity (see Table 1 for aqueous chemistry).

the present study, the cause of death was a combination of respiratory effects (Fig. 2) plus ion losses leading to cardiac failure due to haemoconcentration (Figs. 4B, 4D, and 4F). The decreases in plasma Na and Cl concentration and the ensuing haemoconcentration suggest that Cu was the lethal metal in our Cd and Cu mixture; however, synergistic effects of the combined metal exposure on plasma electrolyte balance have been reported. Pelgrom et al. (1995) reported greater losses in plasma Cl concentrations in tilapia (*Oreochromis mossambicus*) exposed to combined 3.2 μM Cu and 0.6 μM Cd than in tilapia exposed to the same concentrations of each metal separately.

High and low concentrations of DOM protected against the acute effects of the metal exposure on respiratory gas transfer, acid–base balance, and Na and Cl regulation in trout and protected against the accumulation of Cd and Cu in trout plasma. Metals must first bind to fish gills to elicit a toxic effect either directly on the gill or by passing through the gill (Laurén and McDonald 1985). In the presence of DOM, there were fewer Cd and Cu cations present in the water to bind to the gill because of complexation with DOM (see Table 5); thus, Cd and Cu interactions at trout gills were dependent on the relative strength of Cd and Cu binding to the gills and the strength of Cd and Cu binding to DOM (see Table 4). Because Cd and Cu were less available for binding to trout gills in the presence of DOM, the respiratory effects of the metals were eliminated (Fig. 2). Cadmium and Cu in the presence of DOM presumably caused only minor gill damage and therefore resulted in little impairment of respiratory gas transfer, and there was no effect of the metals on ventilation flow or cough rate in the presence of DOM. In addition, there was almost no increase in blood lactate concentrations (Figs. 2C, 2G, and 2K), further indicating no impairment of respiratory gas transfer and therefore no induction of anaerobic glycolysis. The small increase in blood lactate observed in trout exposed to metals plus low natural DOC (Fig. 2G) was possibly due to the reduction in blood Hb and Ht from repetitive blood sampling, resulting in reduced oxygen carrying capacity of the blood. As expected from the lack of hypercapnia and internal lactacidosis, no extracellular acidosis was measured in trout exposed to metals in the presence of DOM (Figs. 2D, 2H, and 2L).

Waterborne metals such as Cu that bind more strongly to DOM compared with the gills will theoretically not accumulate on or in fish gills and therefore will not interfere with ion transport mechanisms. Copper was not observed to accumulate on or in fish gills (Fig. 6B), and our simulations using the modified MINEQL⁺ computer program indicated that <33% of the Cu–gill binding sites were filled with Cu in the presence of either high or low concentrations of DOC (Table 5). The modified MINEQL⁺ model calculated that the majority of the Cu was complexed with DOM, leaving little cationic Cu. Because Cu was inhibited from binding to trout gills in the presence of high and low concentrations of DOC, Cu likely could not bind to Na transport proteins, Na and Cl fluxes at trout gills were therefore not affected, and plasma Na and Cl concentrations did not decrease (Fig. 3). Consequently, there were no reductions in the osmotic potential of the trout blood, and no haemoconcentration was observed in trout exposed to metals plus DOM (Figs. 4B, 4D, and 4F).

Waterborne metals that bind more strongly to fish gills than to DOM, such as Cd, will theoretically accumulate on or in trout gills even in the presence of DOM. Therefore, Cd binding by trout gills could still interfere with ionoregulation in fish even in the presence of DOM. Significant amounts of Cd were accumulated by trout gills exposed to metals plus DOM (Fig. 6A), and MINEQL⁺ simulations indicated that 28–97% of the Cd–gill binding sites were occupied by Cd even in the presence of DOM (Table 5). The modified MINEQL⁺ model calculated that between 31 and 93% of the Cd was complexed with DOM, leaving 3–60% cationic Cd in solution. Of the fish exposed to Cd and Cu plus DOM, most Cd accumulated on the gills of trout exposed to metals plus low natural DOC (Fig. 6A), and there was an associated plasma hypocalcemia in these fish (Fig. 4C).

Cadmium has been demonstrated to affect ionoregulation at freshwater fish gills by interfering with Ca regulation (Wicklund Glynn et al. 1994). The proposed mechanism by which Cd interferes with Ca influx at the gills is through competitive inhibition of the basolateral Ca pump (Verbost et al. 1989). It is possible that the high concentrations of Cd measured at the gills of trout exposed to metals plus low natural DOC (Fig. 6A) were due to Cd binding to high-affinity Ca transport proteins, thus affecting Ca influx, resulting in the observed plasma hypocalcemia (Fig. 4C). Hypocalcemia may have been responsible for the deaths of three of six

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trout exposed to metals plus low natural DOC (see Fig. 4D). Clearly, DOM can protect against the acute respiratory and ionoregulatory effects of metals such as Cd and Cu, but more chronic, ionoregulatory effects caused by the metals, especially Cd, may still occur.

Some studies have suggested the DOM can interact directly with fish gills at low pH, and it has been proposed that these interactions may have implications on metal toxicity (e.g., Wilkinson et al. 1993; Campbell et al. 1997). However, these studies did not indicate if DOM interactions themselves had any deleterious effects on fish. The present study demonstrated that DOM, even at very high concentrations (31 mg C/L DOC), did not cause respiratory or ionoregulatory effects on trout (Fig. 5), in agreement with the results of Goodrich et al. (1991) and Chio et al. (1998). The increase in plasma Cl concentrations observed in trout exposed to metal-free water plus high commercial DOC (Fig. 5C) was probably due to an increase in aqueous Cl from the added humic acid (1600 versus 300 μM Cl) (Table 2), not an effect of the humic acids interacting at the gill. Thus, DOM is protective against the physiological and toxicological effects of metals such as Cd and Cu and has no deleterious effects of its own.

In the present study, DOM was the major chemical parameter protecting against the effects of Cd and Cu on trout. There were some unavoidable increases in aqueous Na, Cl, and Ca concentrations when DOM was added to the exposure water. Although we cannot conclusively exclude these increases as also keeping Cd and Cu from binding to fish gills and reducing the physiological effects of the metals, modelling exercises with the modified MINEQL$^+$ program indicated that the increases in these ions were insignificant compared with the effects of increasing DOM concentration. The large effects of DOM on metal binding to fish gills are due to the high DOM stability constants compared with the low Ca–gill, Na–gill, and metal–Cl stability constants (see Table 4; log K_{CdCl} = 1.9, log K_{CuCl} = 0.1).

In conclusion, we demonstrated that low, environmentally realistic concentrations of natural DOC protected against an acutely toxic combined Cd and Cu exposure of rainbow trout in soft water. The degree of protection afforded by the low concentrations of natural DOC was similar to high concentrations of commercial DOC. DOM protected against the respiratory and ionoregulatory effects of Cd and Cu by binding the metals and reducing the concentrations of cationic Cd and Cu available to bind at the gills and prevented Cd and Cu accumulation in trout plasma. Copper was inhibited from binding to trout gills in the presence of even low concentrations of DOC, while no concentrations of DOC used completely prevented Cd from binding to trout gills. Accompanying elevated gill Cd concentrations even in the presence of added DOM was evidence of plasma hypocalcemia. Finally, the present study demonstrated that DOM, even at very high concentrations, does not cause deleterious ionoregulatory and respiratory effects of its own and is always partially to fully protective against the physiological and toxicological effects of metals such as Cd and Cu.

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Histopathology of adult Pacific herring in Prince William Sound, Alaska, after the *Exxon Valdez* oil spill

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Abstract: Pacific herring (*Clupea pallasi*) sampled from oiled sites in Prince William Sound, Alaska, U.S.A., 3 weeks after the 1989 *Exxon Valdez* oil spill had multifocal hepatic necrosis and significantly increased tissue concentrations of polynuclear aromatic hydrocarbons (PAH). By comparison, Pacific herring from reference sites in 1989 and from all sites in 1990 and 1991 did not have hepatic necrosis or increased PAH concentrations. Adult Pacific herring were sampled for histopathology of liver, spleen, and kidney from oiled and reference sites in April (1989 and 1991) and October (1990 and 1991). Increased scores for macrophage aggregates contributed to significant differences in 1990, but these differences probably resulted from sampling older fish from the oiled site. Naphthalenes were the predominant PAH in all tissue samples. The development of hepatic necrosis and the predominance of naphthalenes in samples from 1989 is consistent with recent laboratory study in which crude oil exposure resulted in dose-dependent expression of viral hemorrhagic septicemia virus (VHSV). We conclude that Pacific herring were exposed to *Exxon Valdez* oil in 1989 and that development of hepatic necrosis in exposed fish probably was a result of VHSV expression.

Résumé : Des harengs du Pacifique (*Clupea pallasi*) échantillonnés à des sites mazoutés dans la baie Prince William, en Alaska (É.-U.), 3 semaines après le déversement d'hydrocarbures de l'*Exxon Valdez* de 1989 ont montré une nécrose hépatique multifocale et des concentrations tissulaires significativement accrues d'hydrocarbures aromatiques polycycliques (HAP). En comparaison, des harengs du Pacifique prélevés en 1989 aux sites témoins et d'autres prélevés en 1990 et 1991 à tous les sites n'ont pas montré de nécrose hépatique ni des concentrations accrues de HAP. À des fins d'examen histopathologique du foie, de la rate et des reins, on a échantillonné des harengs du Pacifique adultes à un site mazouté et à des sites témoins en avril 1989 et 1991 et en octobre 1990 et 1991. Des agrégats de macrophages plus importants ont contribué à établir des différences significatives en 1990, mais ces différences résultent probablement de l'échantillonnage de poissons plus âgés au site mazouté. Les naphtalènes étaient les HAP les plus abondants dans tous les échantillons de tissus. Le développement de la nécrose hépatique et la prédominance des naphtalènes dans les échantillons de 1989 vont dans le sens d'une étude de laboratoire récente dans laquelle l'exposition au pétrole brut a donné lieu à l'expression dépendante de la dose du virus de la septicémie hémorragique virale. Nous concluons que des harengs du Pacifique ont été exposés au pétrole de l'*Exxon Valdez* en 1989, et que le développement de la nécrose hépatique chez les poissons exposés était probablement attribuable à l'expression du virus de la septicémie hémorragique virale.

[Traduit par la Rédaction]

Introduction

The effects of crude oil exposure on organs of adult fish have been documented in several laboratory studies (Hawkes 1977; Khan 1995; Malins 1982; Payne et al. 1978; Solangi and Overstreet 1982), but histopathology of the effects of environmental exposure to oil spills has rarely been documented (Haensly et al. 1982; Khan 1990). When the *Exxon Valdez* oil spill occurred in Prince William Sound, Alaska, U.S.A., in late March 1989, Pacific herring (*Clupea pallasi*) were beginning to congregate in shallow bays for their annual mass spawning in April. Because of the potential for contamination of Pacific herring with *Exxon Valdez* oil, we initiated a study to determine effects of the spill. In 1989, we found that fish from oiled sites had hepatic necrosis and evidence of hydrocarbon exposure, but fish from ref-

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Table 1. Sampling schedule for histopathology and hydrocarbon analysis of adult Pacific herring from Prince William Sound, Alaska, after the March 1989 *Exxon Valdez* oil spill.

Date	Site	Exposure	Histopathology sample size	Hydrocarbon analysis sample size
April 13, 1989	Fairmount Bay	Reference	10	3
April 12, 1989	Galena Bay	Reference	10	3
April 11, 1989	Naked Island	Oiled	10	3
April 14, 1989	Rocky Bay	Oiled	10	3
April 7, 1990	Galena Bay	Reference	ND[a]	3
April 11, 1990	Wells Bay	Reference	ND	3
April 10, 1990	Naked Island	Oiled	ND	3
April 9, 1990	Port Chalmers	Oiled	ND	3
October 6, 1990	Knowles Head	Reference	50	ND
October 10, 1990	Green Island	Oiled	50	ND
April 6, 1991	Galena Bay	Reference	20	ND
April 7, 1991	Granite Bay	Reference	20	ND
April 6, 1991	Montague Island	Oiled	20	ND
October 12, 1991	Green Island	Oiled	49	ND
Oct. 15–17, 1996	Green Island & Zaikof Bay	ND	159	ND

Note: Designation of sites as oiled or unoiled was based on visual evidence of shoreline oil and the presence of polynuclear aromatic hydrocarbons characteristic of *Exxon Valdez* oil in intertidal mussels (Brown et al. 1996). Location of most sites is mapped by Brown et al. (1996); others include Galena Bay (latitude 60°57′, longitude 146°42′), Granite Bay (latitude 60°24′, longitude 147°57′), and Wells Bay (latitude 60°57′, longitude 147°30′). In 1990, tissues for histopathology were sampled from females only; samples for histopathology in 1989, 1991, and 1996 were obtained at random with respect to gender.

[a]ND = no data.

erence sites did not. Study was continued through 1991 to determine the persistence of exposure-related lesions. Some of the histopathology results from Pacific herring sampled in 1989 were reported previously (Moles et al. 1993), and in that report, fish from oiled sites had increased hepatic necrosis, more severe hepatic coccidian parasites (*Goussia* [*Eimeria*] *clupearum*), and decreased numbers of larval herring worms (*Anisakis simplex*) in the peritoneal cavity. These changes were attributed to oil exposure, but hydrocarbon analyses from field-sampled fish were not available.

Since the study of Moles et al. (1993) was published, important new information has become available that may explain their results. First, hydrocarbon analysis of Pacific herring tissues is now complete, and results are reported herein. Second, annual study of Pacific herring in Prince William Sound has documented the variability of various microscopic lesions, particularly pigmented macrophage aggregates (Elston et al. 1997; Kocan et al. 1996; Marty et al. 1998). Third, viral hemorrhagic septicemia virus (VHSV) was first isolated from Pacific herring in Prince William Sound in 1993 (Meyers et al. 1994). VHSV has subsequently been associated with multifocal hepatic necrosis in three different studies (Carls et al. 1998; Kocan et al. 1997; Marty et al. 1998).

Adult Pacific herring were sampled from Prince William Sound after the *Exxon Valdez* oil spill in 1989, 1990, and 1991. The objective of this report is to describe microscopic lesions in these fish and to present mechanisms by which these lesions could be related to crude oil exposure, natural variability, and viral hemorrhagic septicemia. Also, the Pacific herring population of Prince William Sound declined over 80% from an estimated 9.8×10^7 kg in 1992 to 1.5×10^7 kg in 1994. Because fish sampled in the present study were from year-classes that were still alive during this population collapse, these results provide important information on prevalence of parasites and lesions before the epizootic. Even though epizootics are relatively common on a global scale (Hyatt et al. 1997; Sindermann 1990), detailed pre-epizootic information has rarely been available.

Methods

Adult Pacific herring were captured in oiled and reference areas in Prince William Sound using purse seines (Table 1), except for the October 1991 sample from Knowles head, which was trawled. Dates and locations varied for each year because of fish movements, weather conditions, and limited time for study design in 1989. Age (from scales), body weight, and standard length were determined for all but the 1989 and October 1991 samples. When most samples were collected, VHSV had never been isolated from Pacific herring, and virology was not a standard method used in toxic spill damage assessment; therefore, virus isolation was not attempted on any fish sampled from 1989 through 1991. Fish sampled in 1996 were not a part of this study but are reported here solely to demonstrate the relation of age to pigmented macrophage aggregates in the trunk kidney.

Histopathology

Tissues were preserved in Bouin's (1989 samples) or 10% neutral buffered formalin (1990, 1991, and 1996 samples) and shipped to the University of California, Davis. Liver, trunk kidney, and spleen were examined from all samples except in 1989 (when gonads were examined, but spleens were not). Tissues from each fish were assigned a unique random histopathology number for blind study, processed routinely into paraffin, sectioned at 5 μm, and stained with hematoxylin and eosin. Lesions were scored using a four-point scale as none (0), mild (1), moderate (2), or severe (3). For quality control, autolysis and artifact in each spleen were scored on the same four-point scale. Ranking of lesions was often based on the number of inflammatory cells or organisms (e.g., resting spores of *Ichthyophonus hoferi*) per 100× or 400× field on a binocular light microscope. Degenerative and necrotic lesions (e.g.,

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Table. 2. Mean lesion scores in adult Pacific herring captured in April 1989, from oiled and reference sites in Prince William Sound, Alaska.

	Fairmount Bay (reference)	Galena Bay (reference)	Naked Island (oiled)	Rocky Bay (oiled)
Liver lesions				
Hepatocellular glycogen depletion	3	3	3	3
Hepatic lipidosis	0.9	1	0.4	0.6
Coccidiosis (*Goussia clupearum*)	0.5	0.9	0.9	0.9
Ichthyophonus hoferi	0	0.2	0.1	0.1
Pigmented macrophage aggregates	1.9	1.5	2.2	1.8
Focal necrosis	0	0	0.5	0.3
Single cell necrosis	0.3	0.1	0.5	0.5
Hepatocellular megalocytosis	0.8	1.1	0.7	1
Spleen lesions				
Autolysis	2	2	2.3	2.4
Artifact	1	1	1	1
Congestion	1.2	0.8	0.8	0.9
Pigmented macrophage aggregates	2.5	2.6	2.3	2.5
Granulomatous inflammation	0	0	0	0
Ichthyophonus hoferi	0	0.4	0	0
Ellipsoid hypertrophy	0.7	1.8	2.5	1.8
Focal arteriolar intimal hypertrophy	0.2	0.4	0.8	0.1

Note: Lesions were scored as none (0), mild (1), moderate (2), or severe (3).

hepatocellular necrosis) were scored based on the extent of organ involvement (Marty et al. 1998). After all organs were examined and lesions scored, codes were revealed and results were subjected to statistical analysis.

Lesion scores from each year were analyzed separately using similar methods (Marty et al. 1997). Lesion scores were first summarized using principal components analysis. For a given set of scores, the first four principal components were used as a summary for most of the variability in the raw data. The principal component factor scores were then tested for systematic effects of oil exposure using multivariate analysis of variance (MANOVA; Johnson and Wichern 1992). After the MANOVA, univariate ANOVA models were run on each of the individual principal components (Winer et al. 1991). For each analysis, gender and age (or length) effects were also determined. Because the probability of Type I error increases with multiple analyses, ANOVA was not done on scores for individual lesions. Differences in sample prevalence of major parasites were compared using a chi-square test with a 2 × 2 contingency table.

Hydrocarbon analysis

Concentrations of polynuclear aromatic hydrocarbons (PAH) were determined by gas chromatography followed by mass spectrometry for aromatics or flame ionization detection for aliphatics. Analysis was done by the Geochemical and Environmental Research Group at Texas A&M University, College Station, Texas, U.S.A. Experimentally determined method detection limits depended on sample weights and generally were 1 ppb in tissue. Concentrations below method detection limits were treated as 0. The accuracy of the hydrocarbon analyses was about 15% based on comparison with National Institute of Standards and Technology values, and precision expressed as coefficient of variation was usually less than about 20%, depending on the PAH. Total PAH (TPAH) concentrations were calculated by summing concentrations of individual PAH. Tissue concentrations are reported on a wet-weight basis. Not all tissues were collected the same in 1989 and 1990; in 1989, "viscera" was restricted to liver and intestinal ceca, but in 1990, "viscera" included liver and the entire gastrointestinal tract.

Statistical analysis of hydrocarbon results was limited to tissues common to both years (ovary and viscera). TPAH concentrations in ovaries and viscera were independently analyzed with two-way ANOVA (year, site, and year × site). For statistical analysis, differences in viscera collections between 1989 and 1990 were ignored. Comparisons of lesion scores and TPAH concentrations were categorized as not significant ($P > 0.05$), significant ($P \leq 0.05$), or highly significant ($P \leq 0.01$).

Results

Histopathology

In 1989 (Table 2), four Pacific herring from oiled sites (20%) had moderate to severe hepatocellular necrosis, whereas none of the herring from unoiled sites had more than mild necrosis. All four affected fish had single cell necrosis of hepatocytes (or apoptosis) characterized by granular condensed cytoplasm and nuclear pyknosis (Marty et al. 1998). Three of these fish also had moderate or severe, multifocal, coagulative necrosis characterized by rounding-up of individual hepatocytes, cytoplasmic hypereosinophilia, and nuclear karyorrhexis and karyolysis (Fig. 1). Necrotic foci were randomly distributed and sometimes coalesced into large areas. In some areas, necrotic foci were bordered by moderate to large numbers of macrophages that were often in aggregates. Some of these macrophages contained yellow-brown to green cytoplasmic pigment, but most did not contain pigment. Despite these differences, the sample size was small and site differences in 1989 were not significantly different with respect to oiling history of the sample sites (MANOVA). Fish from all sites had several other changes, but none was clearly related to potential oiling of the sample sites: (1) glycogen depletion (all fish); (2) lipidosis; (3) pigmented macrophage aggregates; and (4) karyomegaly, bi- and tri-nucleated hepatocytes (Table 2).

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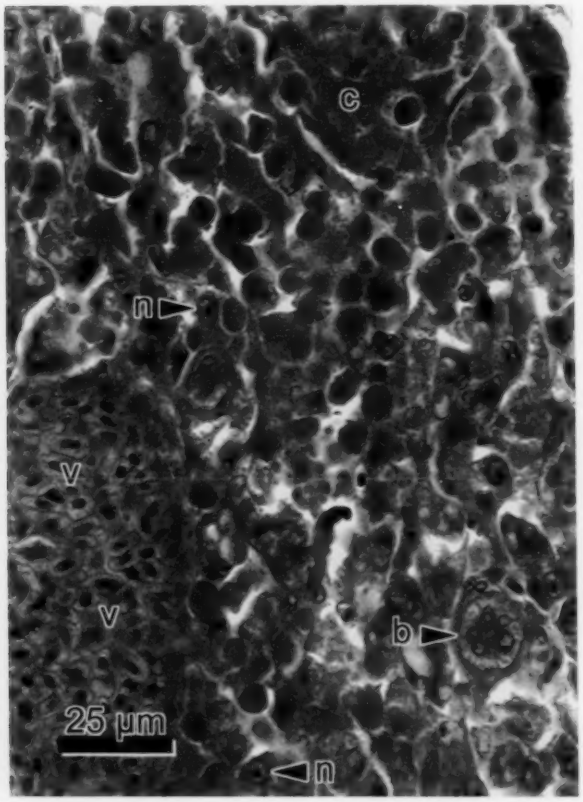
Fig. 1. Liver of a female Pacific herring captured near an oiled site (Naked Island) on April 11, 1989. Viable hepatocytes have normal nuclei (*n*), whereas necrotic hepatocytes have coagulated cytoplasm (*c*) often contracted into an area about the same size as nuclei. A blood vessel (*v*) and bile duct (*b*) are normal.



Oil-related differences in lesion scores were significant in 1990 but not in 1991. None of the Pacific herring sampled in 1990 or 1991 had hepatic necrosis. Instead, the primary tissue change used to separate the sites was pigmented macrophage aggregates (Table 3). In 1990, mean scores for pigmented macrophage aggregates were greater in fish sampled from the previously oiled site. However, fish from the oiled site were older than fish from the reference site (mean age = 5.6 vs. 2.3 years), and mean scores for pigmented macrophage aggregates within each age were similar to mean scores for same-aged fish sampled in October 1996 (Table 4). Also, age differences were significant for 1990 and 1991 samples (MANOVA), and scores for pigmented macrophage aggregates contributed most to significant differences. Gender differences were never significant.

Prevalence of major parasites followed two general trends from 1989 to 1991 (Table 5). First, prevalence of two parasites was stable in 1989 and 1990 but decreased significantly in 1991: *Goussia clupearum* (a coccidian parasite in the liver) and *Ichthyophonus hoferi* (a disseminated fungus, classified by some as a rosette agent or choanoflagellate, see Spanggaard et al. 1996). And second, prevalence of two other parasites increased significantly from 1990 through 1991: the renal myxosporeans *Ortholinea orientalis* and *Sphaerospora* (species not identified). Testis was examined only in 1989: in all sites combined, 93% of the males had the testicular coccidian *Eimeria sardinae*.

Hydrocarbon analysis

Tissue concentrations of TPAH were significantly greater in fish collected from oiled areas in 1989 than in fish collected from reference areas in 1989 and from all areas in 1990. Naphthalenes represented 95–97% of TPAH above method detection limits in these tissues (Tables 6 and 7). In 1989, PAH concentrations tended to be greater in the viscera than in the gonad.

Discussion

Based on recent studies, hepatic necrosis in Pacific herring sampled from oiled sites in 1989 was probably a result of viral hemorrhagic septicemia (VHS), and exposure to *Exxon Valdez* oil might have induced viral expression in subclinical carrier fish. The North American strain of VHSV was first isolated from Pacific herring in Prince William Sound during a severe population decline in 1993, 4 years after the spill (Meyers et al. 1994). A more detailed study in 1994 revealed that VHSV isolation was significantly related to hepatic necrosis (Marty et al. 1998), and this association was confirmed in 38 VHSV-positive fish sampled from Prince William Sound in 1997 (G.D. Marty, unpublished data). The gross lesions in Pacific herring sampled from oiled sites in 1989 (petechiation of the vent and maxillary process (Moles et al. 1993)) are consistent with VHS in juvenile, specific pathogen free, Pacific herring exposed to VHSV in the laboratory (Kocan et al. 1997). Finally, exposure of adult Pacific herring of unknown VHSV status to crude oil in the laboratory resulted in expression of VHSV in a dose-dependent manner, and hepatic necrosis was one of the most severe lesions in exposed individuals (Carls et al. 1998).

Hydrocarbon analysis of Pacific herring tissues in 1989 and 1990 provided weak but statistically significant evidence that fish had been exposed to *Exxon Valdez* oil. The composition of tissue hydrocarbons in Pacific herring from Prince William Sound did not match that of *Exxon Valdez* oil; however, fish rapidly metabolize petroleum hydrocarbons (Collier and Varanasi 1991; Thomas et al. 1997), and tissue hydrocarbon levels may not reflect actual exposure. Naphthalenes are the most likely PAH to be accumulated by Pacific herring exposed to oil-contaminated seawater because they are the most abundant among the PAH in *Exxon Valdez* oil (Short et al. 1996) and they dissolve most readily (Short and Heintz 1997). As evidence, naphthalenes were the most abundant PAH measured in surface seawater along the trajectory of the spill in Prince William Sound during the period when fish were collected in 1989 (Short and Harris 1996). The finding of naphthalenes as the only PAH above method detection limits in tissues is, therefore, expected at the sufficiently low concentrations of less-weathered *Exxon Valdez* oil in seawater. This has been confirmed by evidence from laboratory exposures (M.G. Carls, U.S. National Marine Fisheries Service, Auke Bay, Alaska, personal commu-

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Table 3. Mean age, weight, length, and lesion scores in adult Pacific herring captured in 1990 and 1991 from oiled and reference sites in Prince William Sound, Alaska.

	October 1990		April 1991		October 1991	
	Green Island (oiled)	Knowles Head (reference)	Montague Island (oiled)	Galena Bay (reference)	Granite Bay (reference)	Green Island (oiled)
Measurement						
Age (years)	5.6	2.3	7.2	7.4	7.4	ND[a]
Standard length (mm)	202.1	171.5	221.9	222.5	221.6	ND
Body weight (g)	133.1	68.9	146.9	157.4	143.3	ND
Liver lesions (mean score)						
Hepatocellular glycogen depletion	2	1.9	3	3	3	2.3
Hepatic lipidosis	0.6	0.6	1.1	0.9	1.2	0.5
Coccidiosis (*Goussia clupearum*)	0.8	1	0.7	1	0.8	0.5
Ichthyophonus hoferi	0.1	0.3	0	0	0.3	0
Pigmented macrophage aggregates	1.3	1	2	2.1	1.8	0.9
Focal necrosis	0	0	0	0	0	0
Single cell necrosis	1.1	0.4	0.1	0	0	0.7
Hepatocellular megalocytosis	1.3	1.3	1	1.1	0.8	0.7
Kidney lesions (mean score)						
Pigmented macrophage aggregates	1.5	1	2.1	2.2	1.8	1
Granulomatous inflammation	0.04	0.1	0.2	0.3	0.1	0.04
Interstitial hematopoietic cells	1.1	1	1.1	1.2	1.2	1
Congestion	0.9	0.7	0.3	0.2	0.2	1.2
Ichthyophonus hoferi	0.2	0.2	0	0	0.3	0
Mineralization	0.02	0.02	0	0	0.1	0.1
Tubular epithelial vacuolation	0.1	0.1	0.3	0.2	0.1	0.2
Intraductal myxosporean	0	0	0.2	0.1	0.1	0
Ortholinea orientalis	0.2	0.2	0.5	0.4	0.2	0.5
Spleen lesions (mean score)						
Autolysis	0.2	0.1	0.1	0	0	0.2
Artifact	1	1	1	1.1	1	1
Congestion	1.3	1	0.7	0.5	0.3	1
Pigmented macrophage aggregates	1.6	1.1	2.3	2.7	2.7	1
Granulomatous inflammation	0.1	0	0	0.1	0.2	0.04
Ichthyophonus hoferi	0.2	0.2	0	0	0.1	0.02
Ellipsoid hypertrophy	1	0.7	1.5	1.4	1.3	1
Focal arteriolar intimal hypertrophy	0.1	0.1	0.5	0.6	0.6	0.3

Note: Lesions were scored as none (0), mild (1), moderate (2), or severe (3).
[a]ND = no data.

Table 4. Semiquantitative scores for pigmented macrophage aggregates in the trunk kidney of adult Pacific herring randomly sampled from Prince William Sound, Alaska, after the March 1989, *Exxon Valdez* oil spill.

	October 1990						October 1996		
	Green Island			Knowles Head			Green Island and Zaikof Bay		
Age	*n*	Mean	SE	*n*	Mean	SE	*n*	Mean	SE
2	0	NC[a]	NC	42	0.95	0	66	1.15	0.06
3	2	1	0	1	2	NC	31	1.19	0.1
4	2	1.5	0.5	3	1	0	29	1.24	0.08
5	13	1.31	0.1	2	1.5	0.5	5	1.4	0.24
6	19	1.63	0.1	0	NC	NC	6	1.67	0.21
7	4	1.75	0.3	0	NC	NC	9	2	0.24
8	0	NC	NC	0	NC	NC	10	2.1	0.18
10	0	NC	NC	0	NC	NC	1	3	NC
12	0	NC	NC	0	NC	NC	2	3	0
All	40			48			159		

Note: Pigmented macrophage aggregates were scored as none (0), mild (1), moderate (2), or abundant (3). The 1988 year-class were 2-year-olds in 1990 and 8-year-olds in 1996.
[a]NC = not able to calculate.

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Table 5. Sample prevalence (%) of major parasites in Pacific herring sampled from Prince William Sound, Alaska.

Sample date	*Goussia clupearum*	*Ichthyophonus hoferi*	Renal intraductal myxosporean (*Sphaerospora* sp.?)	*Ortholinea orientalis*
April 1989	63	13	NE[a]	NE
October 1990	60	15	0	12
April 1991	54	3.4	2.4	20
October 1991	40	2.1	8.2	31

Note: Samples are the same as in Tables 2 and 3. Because there were no significant differences among site of capture and sample size for each site was small, data from all sample sites are combined.
[a]NE = kidney was not examined.

Table 6. Hydrocarbon concentrations (ng hydrocarbon/g tissue) in Pacific herring sampled from oiled and reference sites in April, 1989.

		Viscera		Gonad	
Class		Reference	Oiled	Reference	Oiled
Total aromatics	Mean	92.9	155.3	17	41.9
	SE	16.3	42.6	2.2	16.9
Naphthalenes	Mean	89.1	143.9	17	38
	SE	16.9	37.9	2.2	18.5
Fluorenes	Mean	0	1.5	0	0
	SE	0	1.5	0	0
Phenanthrenes	Mean	0	3.6	0	0
	SE	0	2.3	0	0

Note: For all determinations, $n = 6$ except for gonads from oiled sites, where $n = 3$. Concentrations less than method detection limits are reported as 0. In all samples, concentrations of dibenzothiophenes and chrysenes were less than method detection limits.

Table 7. Hydrocarbon concentrations (ng hydrocarbon/g tissue) in adult Pacific herring sampled from oiled and reference sites in April, 1990.

		Viscera		Ovary		Testes		Stomach contents		Muscle	
Class		Reference	Oiled	Reference	Oiled	Reference	Oiled	Reference	Oiled	Reference	Oiled
Aromatics	Mean	22.6	6.1	11	0.7	0	0	19	4	6.9	5.5
	SE	4.3	4.1	6.1	0.7	0	0	11.4	6.8	4	2.6
Naphthalenes	Mean	20.9	6.1	11	0.7	0	0	19	4	6.9	5.5
	SE	3.9	4.1	6.1	0.7	0	0	11.4	6.8	4	2.6

Note: $n = 6$ for all oiled sites, and $n = 4$ for all reference sites). Concentrations of fluorenes, dibenzothiophenes, phenanthrenes, and chrysenes were less than method detection limits. None of the site differences was statistically significant.

nication). However, some of the naphthalenes in Pacific herring from oiled areas in 1989 may be due to spurious naphthalene from unknown sources, as indicated by the presence of naphthalenes in samples collected from reference areas in 1989 and from all areas in 1990. Alternatively, movements of adult herring in the weeks and months after the spill are not known, and fish collected from reference sites may have been exposed to oil during their migrations. Unexplained elevations in naphthalene concentrations have occurred elsewhere in samples collected for Natural Resource Damage Assessment (J.W. Short, U.S. National Marine Fisheries Service, Auke Bay, Alaska, personal communication). Corroborative evidence that Pacific herring were exposed to *Exxon Valdez* oil includes contaminated or possibly contaminated bile in two of two herring examined in 1989 (Haynes et al. 1995).

Although oil-related differences in histopathology scores were statistically significant in samples collected in October 1990, these difference may have resulted more from differences in age between the two samples than to exposure histories. Macrophage aggregates were significantly greater in fish from the previously oiled site, and increased numbers of macrophage aggregates have been associated with exposure to oil (Haensly et al. 1982) and other toxicants (Wolke 1992). However, scores for macrophage aggregates in Pacific herring from Prince William Sound in 1994 were highly variable (Elston et al. 1997) and strongly related to increased age (Marty et al. 1998). The highly significant correlation of age and increased scores for macrophage aggregates was confirmed in Pacific herring from Sitka Sound, Alaska, in 1995 and 1996, and the trend continues in ongoing semiannual studies of Pacific herring in Prince William Sound through 1998 ($n = 250 \cdot \text{site}^{-1} \cdot \text{year}^{-1}$; G.D. Marty, unpublished data).

Prevalence of parasites changed over time, but the relationship of these changes to potential oil exposure is not known. It is unlikely that the oil spill affected parasite prevalence or scores other than *Anisakis simplex* in 1989. As supporting evidence, in a laboratory study of adult Pacific herring, neither prevalence nor severity of *Goussia clupearum* or *Ichthyophonus hoferi* was significantly altered by a 16-day oil exposure (Carls et al. 1998). The relatively

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small size of each sample limits our ability to extrapolate sample prevalence to population trends. However, prevalences of most major parasites in 1990 samples were within the range found in Pacific herring from Prince William Sound in more extensive annual surveys from 1994 through 1997, although the prevalence of *Ichthyophonus hoferi* in 1990 was significantly lower than in years after 1993 (Marty et al. 1998, G.D. Marty, unpublished data). In 1991, prevalences of *Goussia clupearum* and *Ichthyophonus hoferi* were unusually low compared with other years in both Prince William Sound and Sitka Sound. By comparison, 1991 prevalence of *Ortholinea orientalis* was unusually high, particularly in the October sample. Study continues to determine the prevalence of various parasites in Prince William Sound Pacific herring, and future results from year-classes unaffected by the oil spill may provide valuable information for interpreting the significance of trends observed from 1989 through 1991.

In summary, adult Pacific herring in Prince William Sound were likely exposed to *Exxon Valdez* oil in April 1989, but fish no longer had significant evidence of exposure in 1990. Because Pacific herring near spawning condition in early spring are in a state of physiological stress, the added stress of oil exposure in 1989 could reasonably have led to expression of VHSV in these fish. Stress-induced expression of VHSV in Prince William Sound Pacific herring probably occurred in April of 1989. VHSV has been isolated from Pacific herring throughout the Pacific Northwest (Meyers and Winton 1995), and preliminary evidence indicates that about 10% of Pacific herring carry VHSV in subclinical form (R.M. Kocan, University of Washington, Seattle, Wash., personal communication). The potential for development of VHS in carrier-fish subjected to additional stress makes Pacific herring unusually sensitive to effects of crude oil if exposure occurs in the weeks before spawning. However, we have no evidence that a VHSV outbreak resulted in a significant decline in population biomass in 1989. The population biomass was at near record levels in 1989 and remained fairly stable until it collapsed in 1993. Lesion prevalences in fish sampled in 1990 or 1991 were essentially within normal limits, and there was no direct evidence to link the population collapse in 1993 to the 1989 oil spill (Elston et al. 1997; Marty et al. 1998; Meyers et al. 1994). This study was limited by relatively small sample size, particularly in 1989, as well as by the large gap between the April 1989 and October 1990 samples. Also, the potential role of VHSV in Pacific herring was unknown before 1993 and, therefore, was not initially considered as a significant variable. Based on these findings, the immediate response to large toxicant spills in the future should include adequate sample size and consideration of the potential interaction of multiple stressors in exposed individuals.

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Assessing the strength of top-down influences on plankton abundance in unmanipulated lakes

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Abstract: The trophic structure of aquatic ecosystems can potentially be controlled by two sets of factors: resource availability and predation. The importance of nutrients was demonstrated by two observations: first, that plankton abundance among lakes is strongly correlated with resource levels, and second, that experimental manipulations of resources lead to changes in plankton abundance. In contrast, while experimental manipulations have shown that predators can affect prey abundance, it is less clear whether variation in plankton abundance among lakes is related to variation in predators. To test this, we sampled 29 lakes in Quebec and Ontario. We found strong relationships between plankton biomass and resource levels. Effects of predation were evident between zooplankton and phytoplankton. However, neither chlorophyll nor zooplankton biomass was related to piscivorous fish presence, after controlling for phosphorus. Other published studies that have reported correlations between plankton abundance and characteristics of the fish community failed to control for trophic status. Thus, there appears to be no published correlative evidence that variance in plankton abundance among lakes is related to variation in fish assemblages, even though the link is mechanistically plausible.

Résumé : La structure trophique des écosystèmes aquatiques dépend potentiellement de deux facteurs : la disponibilité des ressources et la prédation. L'importance des ressources était mise en évidence par deux faits : la variabilité de l'abondance du phytoplancton parmi les lacs est fortement corrélée avec les concentrations d'éléments nutritifs et les manipulations expérimentales des nutriments peuvent provoquer des changements d'abondance du phytoplancton. Par contre, bien que des expériences aient démontré que les prédateurs puissent affecter l'abondance du plancton, il existe peu de données à l'effet que la variabilité naturelle de l'abondance du plancton soit corrélée avec la prédation. Nous avons testé cette hypothèse en échantillonnant 29 lacs du Québec et de l'Ontario. Nous avons observé de fortes corrélations entre la biomasse du plancton et la disponibilité des ressources. Des effets de la prédation étaient évidents entre le zooplancton et le phytoplancton. Pourtant, ni la concentration de chlorophylle ni la biomasse zooplanctonique ne dépend de la présence de poissons piscivores, si on tient compte d'abord de l'effet des nutriments. D'autres études qui avaient signalé des corrélations entre l'abondance du plancton et des caractéristiques des communautés de poissons n'ont pas tenu compte de l'effet des nutriments. Nous concluons qu'il n'existe aucune indication probante que la variabilité naturelle de l'abondance du plancton dépende des poissons, bien que des expériences aient mis en évidence que cette interaction soit possible.

Introduction

The factors governing the structure of natural food webs have been the subject of intense study for several decades, for reasons of both fundamental and practical interest. "Bottom-up" or resource-controlled models of ecosystem trophic structure suggest that nutrient availability determines plant growth and abundance, which in turn determine herbivore growth and abundance, and so on, up the food web. "Top-down", "trophic cascade", or predator-controlled models (Carpenter and Kitchell 1985, 1992) emphasize the effect of predators on the biomass and productivity of lower trophic levels. For example, Hairston et al. (1960) suggested that the world is green because carnivores prevent herbivores from fully exploiting plant biomass.

On the management level, these two models present two very different strategies to control the abundance of nuisance organisms: manipulation of the food supply versus manipulation of the predators. In aquatic systems, the classical resource-based means to control algal abundance is to reduce nutrient inputs (Edmonson 1991). In contrast, the predator-based hypothesis predicts that an increase in the abundance of piscivorous fish should reduce the abundance of planktivorous fish. This in turn should allow zooplankton (the planktivores' prey) to increase in abundance, which then graze down phytoplankton. It has been suggested that artificially increasing the top predators in pelagic systems may be a cost-effective means of controlling nuisance algal growth (Shapiro and Wright 1984), either by itself or in addition to nutrient control.

The importance of nutrients on plankton abundance was effectively demonstrated by two observations. First, it was shown that much of the variance among lakes in the abundance of algae (Dillon and Rigler 1974) and other aquatic organisms is related to nutrient levels. Second, manipula-

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Table 1. Range of conditions encountered in the 29 lakes sampled in Quebec and Ontario, Canada.

Factor	Range
Temperature (°C)	19.5–24.1
Conductivity (μmho·cm^{-2})	18.2–273
Alkalinity (mequiv.·L^{-1})	20.1–2560
pH	6.0–8.8
Secchi depth (m)	1.3–7.5
Surface area (ha)	1.3–4700
Mean depth (m)	0.6–21.9
Maximum depth (m)	1.8–95
Total phosphorus (μg·L^{-1})	5.5–27
Total chlorophyll *a* (μg·L^{-1})	1.3–14
Zooplankton biomass (mg dry weight·L^{-1})	5.8–408
Crustacean biomass (mg dry weight·L^{-1})	36.8–334
Cladoceran biomass (mg dry weight·L^{-1})	0.211–238
Mean individual log zooplankton dry weight (μg)	–0.975 to –0.077
Variance of Individual log zooplankton dry weight (μg^2)	0.086–0.76

tions of nutrient levels were shown to produce changes in organisms' abundances (Schindler 1977; Edmonson 1991).

The putative effects of predators on the abundance of aquatic organisms are more controversial (Carpenter and Kitchell 1992; DeMelo et al. 1992). There is little doubt that experimental manipulation of predators can produce dramatic effects on phytoplankton and zooplankton biomass (e.g., Mazumder et al. 1988). However, it does not always do so: other experimental studies have found little effect of fish manipulation on phytoplankton and zooplankton biomass (e.g., McQueen et al. 1990). Larger-scale biomanipulation has also had mixed results. An aggressive salmonine stocking program in Lake Michigan was followed by improvements in water quality (Scavia et al. 1986; but see Evans 1992). In contrast, similar salmonine stocking in Lake Ontario did not lead to changes in chlorophyll levels (Lean et al. 1990).

Moreover, in contrast with the situation for resources, little attention has been paid to the question of whether variation in prey abundance among lakes is related to variation in predator densities, after accounting for nutrients. A few studies have looked for relationships between the variation in planktonic prey abundance among lakes and characteristics of the predator assemblages (Mills and Schiavone 1982; Pace 1984; Quirós 1990; Carpenter et al. 1991; Persson et al. 1992; Mazumder 1994). We will closely reexamine these published studies below.

The purpose of the present study is to test whether plankton biomass and size structure in lakes that have piscivorous fish differ statistically from those in lakes without piscivorous fish, after controlling for differences in trophic status. We purposefully examine lakes that have not been experimentally manipulated; insofar as any system is ever at equilibrium, the plankton and fish communities of these lakes presumably are at equilibrium with one another. In a companion study (Wilson 1996), we examined a series of lakes along a gradient of piscivorous fish stocking intensity. The fundamental questions are the same in both cases: how much of the variation in the abundance of the plankton among lakes can be related to predators, after controlling for trophic status?

Materials and methods

Study area

A total of 29 lakes in western Quebec and eastern Ontario were sampled during the summer of 1991. Ten of the 29 lakes had no piscivores. The lakes were selected to include only a moderate range of other characteristics in order to avoid large variation in variables that might be collinear with predator presence/absence (e.g., morphometry or trophic status).

About two thirds of the lakes are in protected areas with restricted public access. Twenty-three of the study lakes are on the Canadian Shield, either in Gatineau Park north of Ottawa, Ontario (Lakes Black, Brown, Carmen, Fortune, Harrington, Kidder, Kingsmere, LaPêche, LeBlanc, Loutre, Meech, Mulvihill, Petit Renaud, Philippe, Ramsey, Renaud, Taylor, Vase) or near St-Hippolyte, Quebec (Lakes Croche, Cromwell, Geai, Pin Rouge, Triton). The remaining six lakes are in the St. Lawrence Lowlands near Kingston, Ontario (Lakes Big Rideau, Gould, Lower Beverley, Opinicon, Sydenham, Upper Beverley).

Descriptions of the morphometry and fish community composition of most of these lakes are given in Chapleau et al. (1997) and Comeau and Boisclair (1998). The lakes containing piscivorous fish in our study area generally contained either trout (brook trout (*Salvelinus fontinalis*) or lake trout (*Salvelinus namaycush*)) or a mixture of bass (largemouth bass (*Micropterus salmoides*) and (or) smallmouth bass (*Micropterus dolomieu*)), yellow perch (*Perca flavescens*), northern pike (*Esox lucius*), and walleye (*Stizostedion vitreum*).

Since the purpose of this study was to examine differences among lakes and not within given lakes, and since seasonal variation of the limnological properties of lakes is typically much smaller than the variation among lakes (Carpenter et al. 1991), sampling concentrated on interlake variation. Each of the lakes (except two) was sampled twice during midsummer stratification from June to September when the biology and chemistry of the lakes are relatively stable.

Sampling

Small- and moderate-sized lakes were sampled at the centre of the lake. Larger lakes were sampled offshore at depths no greater than 15 m. Secchi depth, epilimnion depth, and conductivity were determined with a YSI salinity–conductivity–temperature meter and dissolved oxygen with a YSI oxygen meter. Integrated epilimnetic water samples were taken using an 8-m length of 2.5-cm-diameter Tygon tubing. The water samples were returned to the laboratory and analyses begun within 4 h. A subsample of each of these bottles was used to determine total phosphorus and chlorophyll *a*.

Integrated zooplankton samples were taken using a diaphragm pump connected to an 8-m-long hose 2.5 cm in diameter. The hose was drawn repeatedly through the water column, from either 8 m depth or 0.5 m above the lake bottom, to the water surface. The outflow was passed through a 35-μm Nitex net to gather the zooplankton. The zooplankton were then transferred to a small container and preserved in a sucrose–formalin solution with a final concentration of 4% formalin (Pace 1984). The volume of water thus sampled was calculated from the pumping rate and the time of pumping.

Morphometric variables such as lake surface area, mean depth, and maximum depth were obtained from various published and unpublished sources (Ontario Ministry of the Environment 1985; Lafond et al. 1990; Chapleau et al. 1997).

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Table 2. Resource-based relationships: summary of simple linear regression statistics relating chlorophyll *a* concentration (Chl *a*, $\mu g \cdot L^{-1}$) and the biomass (B, $mg \cdot L^{-1}$) or mean individual dry weight (DW, μg) of components of the zooplankton (microzooplankton, cladocerans, crustaceans, and total zooplankton) to resource availability, including total phosphorus (TP, $\mu g \cdot L^{-1}$).

Dependent variable	Independent variable	Slope	*Y*-intercept	*r*	*p*
Biomass relationships					
log Chl *a*	log TP	+1.05	+0.61	0.85	<0.001
log Microzooplankton *B*	log TP	+0.37	+0.91	0.54	0.003
log Cladoceran *B*	log TP			–0.11	ns
log Crustacean *B*	log TP			–0.11	ns
log Zooplankton *B*	log TP			0.02	ns
log Microzooplankton *B*	log Chl *a*	+1.08	+0.52	0.39	0.04
log Cladoceran *B*	log Chl *a*			–0.34	ns
log Crustacean *B*	log Chl *a*			–0.32	ns
log Zooplankton *B*	log Chl *a*			–0.25	ns
Size relationships					
Zooplankton DW	log TP	–0.61	+0.05	–0.58	<0.001
Var(Zooplankton DW)	log TP	–0.50	+0.90	–0.61	<0.001
Zooplankton DW	log Chl *a*	–0.52	–0.36	–0.60	<0.001
Var(Zooplankton DW)	log Chl *a*	–0.39	+0.56	–0.59	<0.001

Note: Var(Zooplankton DW) denotes the variance in individual dry weight. In all cases, $n = 28$. ns, not significant ($p > 0.05$).

Total phosphorus concentration was measured in quadruplicate 50-mL subsamples, digested with potassium persulfate, and analysed using the molybdenum blue method of Menzel and Corwin (1965). The water samples were not prefiltered to remove larger particles.

Chlorophyll *a* concentration in four size fractions was measured. Total chlorophyll *a* concentration was determined by filtering 250–500 mL of lake water on a Whatman GF/F filter under low vacuum pressure. Next, lake water was filtered sequentially through a 35-μm Nitex filter and 12-, 2.0-, and 0.2-μm polycarbonate filters (Poretics corporation, Livermore, Calif.). These filters were then frozen. Chlorophyll *a* was later extracted in 95% ethanol for about 24 h and then assayed spectrophotometrically (Ostrofsky and Rigler 1987).

For each lake, between 100 and 200 individual zooplankton were counted and their body lengths measured using a microscope and a microcomputer-based caliper system. Individuals were classified as cladocerans, copepods, nauplii, or rotifers. Individual dry weight was estimated using the mass–length regression for zooplankton reported by Peters and Downing (1984).

Fish composition of Gatineau Park lakes was determined by Chapleau et al. (1997). For the non-Gatineau lakes, A. Keast (Biology Department, Queen's University, Kingston, Ont.) and D. Boisclair (Département de Sciences Biologiques, Université de Montréal, Montréal, Qué.) provided unpublished data on the presence/absence of piscivores.

Statistical methodology

Most variables were approximately lognormally distributed; these variables were therefore log transformed to stabilize their variance and to linearize the relationships. The hypotheses that zooplankton biomass and individual body size depend upon chlorophyll *a* or phosphorus concentrations were tested by simple linear regressions. The hypotheses that chlorophyll *a* concentration, zooplankton biomass, and zooplankton individual body size are related to the presence or abundance of piscivorous fish were tested by ANCOVA, controlling for the logarithm of the total phosphorus concentration.

The estimate of zooplankton biomass in one lake, Petit Renaud, proved to be an order of magnitude lower than that of any other lake. Petit Renaud's mean zooplankton biomass was almost four standard deviations below the global mean ($t = 3.92$, $p = 0.001$). Presumably, this means that an unidentified methodological error caused zooplankton to be undersampled in Petit Renaud. Petit Renaud was therefore excluded from statistical analyses involving zooplankton.

Since we report nonsignificant relationships below, it is important to provide information about their power. Rather than estimate power per se, we report minimum detectable effect sizes, given the sample sizes in our study, by estimating the residual sums of squares that a variable added to a general linear model must statistically explain in order to be significant at $p < 0.05$.

Results

Our study sites represented a moderate range of trophic, morphometric, and physicochemical conditions (Table 1). The lakes are mainly oligo- to mesotrophic, low alkalinity, and mainly fairly small. Chlorophyll *a* concentrations vary by an order of magnitude among lakes.

Piscivorous fish presence/absence was unrelated to trophic status (total phosphorus) in this data set (logistic regression, $p = 0.81$, $n = 28$). Lakes with piscivores in our data set tended to be somewhat deeper (median depth of 5.6 m) than lakes without piscivores (median depth of 3.6 m), although this difference was not statistically significantly (logistic regression, $p = 0.096$, $n = 28$). To ensure that depth differences did not confound our analyses of piscivore effects, we repeated all analyses reported below, after eliminating all piscivore lakes deeper than the deepest piscivore-free lake (reducing the set of piscivore lakes from 19 to 11). All results were qualitatively identical to those done with the entire data set; therefore, we present only the results on the whole data set.

Resource-based relationships

Log chlorophyll *a* was strongly related to log total phosphorus in this data set (Table 2; Fig. 1A), as it is in many

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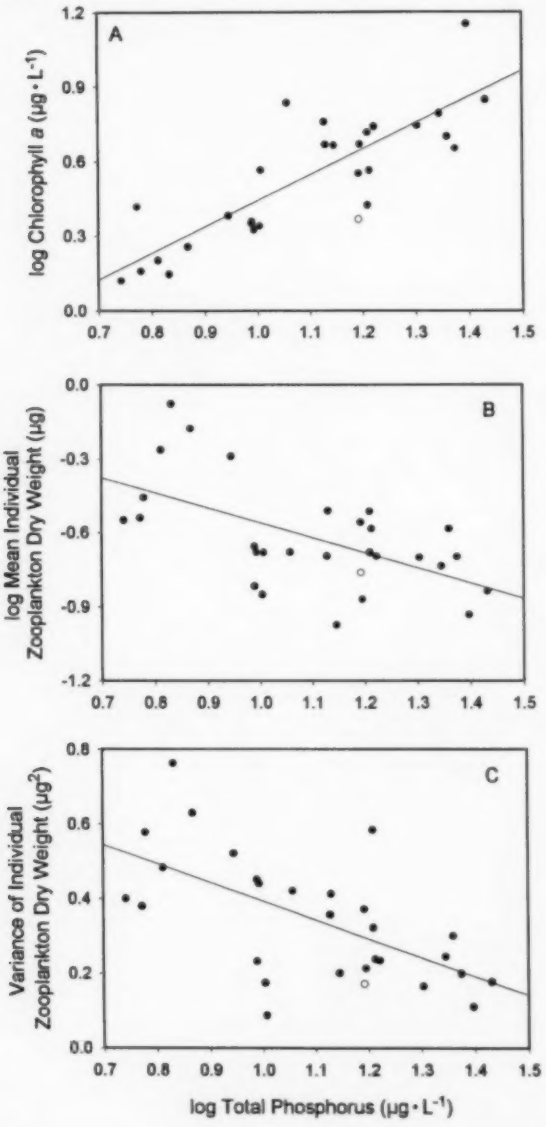
Fig. 1. Resource-based relationships. (A) Relationship between summer total chlorophyll *a* concentration and summer total phosphorus concentration ($r = 0.85$, $n = 28$, $p < 0.001$). (B) Relationship between mean individual zooplankton dry weight and mean summer total phosphorus concentration ($r = -0.58$, $n = 28$, $p < 0.001$). (C) Relationship between the variance of individual zooplankton dry weight and mean summer total phosphorus concentration ($r = -0.61$, $n = 28$, $p < 0.001$). The lines represent the regression models fitted to these data. The open circles represent the data for Petit Renaud. These data were not used in the statistical analyses (see text) but are provided for comparison.



other published studies (Dillon and Rigler 1974). The only component of zooplankton biomass that was clearly related to either total phosphorus or phytoplankton biomass was microzooplankton biomass, which was higher in richer lakes (Table 2). Crustacean zooplankton biomass and total zooplankton biomas, were unrelated to lake trophic status. This contrasts with at least some published results (reviewed and discussed below).

However, zooplankton community size structure was clearly related to trophic status. In richer lakes, zooplankton in general and cladocerans in particular were smaller (Table 2; Fig. 1B). Zooplankton communities in richer lakes also tended to be more uniform in size, as indicated by the significant negative relationship between the variance in individual zooplankton dry weight and log total phosphorus and the variance in individual zooplankton dry weight and log chlorophyll *a* (Table 2; Fig. 1C).

Predator-based relationships

Evidence of predator effects would be found in cases where the abundance of any particular trophic level is negatively related to the abundance or biomass of its predators, after controlling for trophic status. In our data, we find clear evidence consistent with the hypothesis that, when zooplankton biomass is higher, algal biomass is lower (Table 3). Algal biomass is unrelated to zooplankton size, in contrast to the results of Pace (1984).

Effects of the presence or absence of piscivorous fish on the biomass of lower trophic levels are equivocal, at best. Neither algal (Fig. 2) nor zooplankton biomass (Fig. 3) was significantly related to piscivorous fish presence (Table 3). There was a marginally significant ($p = 0.04$) positive relationship between piscivore presence and cladoceran biomass, and possibly a weak negative one with microzooplankton biomass ($p = 0.11$). However, both of these relationships become nonsignificant if one controls for experimentwise error rates (i.e., controlling for the large number of correlations tested).

Clearer evidence of the effects of the presence of piscivorous fish is evident in the size distribution of the zooplankton. When piscivores are present, cladocerans are larger ($p < 0.002$), zooplankton in general may be a bit larger ($p = 0.054$), and zooplankton size is much more variable ($p = 0.005$) (Table 3; Fig. 3). No effect of fish is seen at the level of the phytoplankton size: the distribution of chlorophyll *a* among size fractions did not differ between lakes with or without piscivorous fish (Fig. 2; for the fish × size interaction, $F_{3,103} = 1.50$, $p = 0.22$).

Interactions of trophic status and predators

It has been hypothesized that top-down effects should be strongest in oligotrophic lakes (McQueen et al. 1986), in mesotrophic lakes (Elser and Goldman 1991; Agustí et al. 1992), or in eutrophic lakes (or at least lakes with low seston carbon to phosphorus ratios, Sterner and Hessen 1994). We tested this suite of hypotheses by constructing predator-based ANCOVA models that included the interaction of total phosphorus and characteristics of the predator trophic level. For example, an interaction between phosphorus concentration and piscivore presence/absence tests the hypothesis that piscivores influence the dependent variable differently in lakes of different trophic status. An interaction with a squared log phosphorus term was used to detect nonlinear interac-

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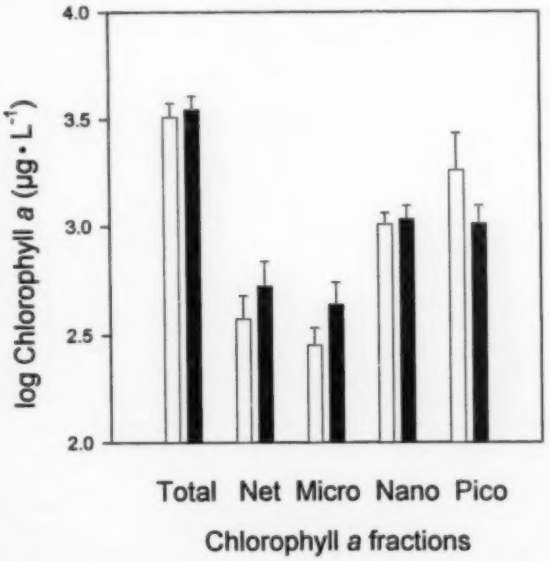
Table 3. Predator-based relationships: summary of results of one-way ANOVA models (n = 28) testing the joint effects of total phosphorus and of a predator on chlorophyll *a* concentration (Chl *a*) or the biomass (B) or mean individual dry weight (DW) of components of the zooplankton (including total zooplankton, crustaceans, cladocerans, and microzooplankton).

	Total phosphorus		Predator		
Dependent variable	Partial r	p	Variable	Partial r	p
Biomass relationships					
log Chl *a*	0.72	<0.001	log Microzooplankton *B*		0.42
log Chl *a*	0.75	<0.001	log Cladoceran *B*	–0.22	0.014
log Chl *a*	0.74	<0.001	log Crustacean *B*	–0.18	0.03
log Chl *a*	0.77	<0.001	log Zooplankton *B*	–0.24	0.009
log Chl *a*	0.72	<0.001	Piscivore +/–		0.96
log Microzooplankton *B*	0.33	0.002	Piscivore +/–	(–0.10)	0.11
log Cladoceran *B*		0.50	Piscivore +/–	0.16	0.04
log Crustacean *B*		0.52	Piscivore +/–	(+0.09)	0.13
log Zooplankton *B*		0.96	Piscivore +/–		0.41
Size relationships					
log Chl *a*	0.72	<0.001	Cladoceran DW		0.87
log Chl *a*	0.58	<0.001	Zooplankton DW	(–0.07)	0.18
log Chl *a*	+0.72	<0.001	Var(Zooplankton DW)		0.39
Cladoceran DW	–0.46	0.000	Piscivore +/–	0.31	0.002
Zooplankton DW	–0.38	0.001	Piscivore +/–	(+0.14)	0.054
Var(Zooplankton DW)	–0.47	<0.001	Piscivore +/–	+0.27	0.005

Note: Piscivorous fish presence or absence is denote by Piscivore +/–. The partial correlation (partial r) is indicated in cases where the relationship was significant at $p \leq 0.05$. We show in parentheses the direction of effects for which $0.05 \leq p \leq 0.2$ in order to suggest relationships that might have been detected with higher sampling intensity.

Fig. 2. Mean summer chlorophyll *a* concentration in lakes lacking (open bars, n = 9) versus having piscivorous fish (solid bars, n = 19). Confidence intervals represent ± 1.0 SE. Total chlorophyll is shown as well as chlorophyll in the following size classes: Net, >35 μm; Micro, 12–35 μm; Nano, 2.0–12 μm; Pico, 0.2–2.0 μm. In no case is the chlorophyll concentration significantly different between lakes with versus without piscivores.



tions (e.g., predator effects that first increase and then decrease along a trophic gradient). We did not observe any evidence of changing effects of piscivory as a function of trophic status for any of the variables that we examined (Table 4).

Power

When a study fails to demonstrate significant relationships, this can mean either that such relationships truly do not exist or that there was insufficient statistical power to detect those relationships that do exist. With the sampling effort used in this study (28 lakes), it can be shown that we should have been able to detect any relationship that statistically accounts for ≥14.5% of the unexplained variance in any given dependent variable. Thus, we can state with certainty that, although zooplankton biomass is not significantly related to total phosphorus, if a relationship truly did exist, then the relationship could not account for more than 14.5% of the variance in log zooplankton biomass (observed in our data set). In the case of predator-based relationships, nonsignificant predator variables cannot explain more than 14.5% of the residual variation, after controlling for phosphorus. Thus, for example, fish presence/absence could not account for ≥4.1% of the total variance in chlorophyll *a* concentration, or our sampling design would have detected the effect. In every other case, predator presence/absence could only potentially account for a relatively small portion (<10–14%) of the total variance in zooplankton variables.

Discussion

Plankton biomass and size structure vary markedly among

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Fig. 3. (A) Mean summer zooplankton biomass in lakes lacking (open bars, $n = 9$) versus having piscivorous fish (solid bars, $n = 19$). Confidence intervals represent ± 1.0 SE. Micro, microzooplankton biomass; Cladoc, cladoceran biomass; Crust, crustacean zooplankton biomass; Total, total zooplankton biomass. All biomass measures were log transformed. (B) Mean and variance of individual zooplankton dry weight (an index of size structure). Variables that differ significantly between lakes with and without piscivorous fish ($p < 0.05$) are denoted by asterisks.

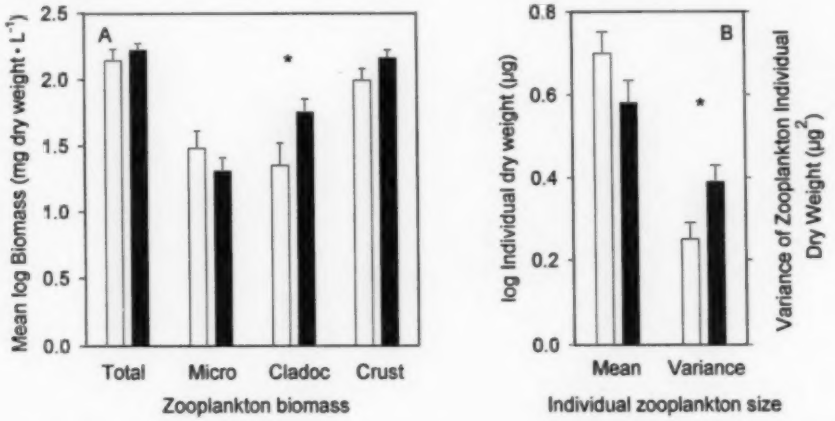

Table 4. Do the effects of piscivorous fish depend upon trophic status? Significance levels (i.e., p values) obtained from ANCOVA's examining the effect of log total phosphorus concentration (log TP) and the presence or absence of piscivorous fish (PISC) on plankton biomass for a set of 29 lakes.

Dependent variable	log TP	PISC	PISC × log TP
log Chlorophyll *a* concentration	0.001	0.67	0.66
log Microzooplankton biomass	0.023	0.48	0.33
log Cladoceran biomass	0.51	0.17	0.29
log Crustacean zooplankton biomass	0.56	0.24	0.33
log Total zooplankton biomass	0.18	0.12	0.14
Zooplankton mean dry weight	0.13	0.06	0.11
Variance in dry weight	0.53	0.04	0.1

Note: The lack of significant interaction (PISC × log TP) indicates that the effects of piscivores do not differ among lakes of differing trophic status in this data set. Models that included a polynomial interaction term ($PISC^2$ × log TP) were also tested; no significant polytonic interactions were observed.

lakes. Much of the variance is related to variation in nutrient availability. Both the present study and many other published studies show this. Typically, these resource-based relationships are strong at the level of phytoplankton, weaker at the level of zooplankton, and nonsignificant at the level of fish (Table 2) (also see Mills and Schiavone 1982; Pace 1984; Prairie et al. 1989; Quirós 1990; Persson et al. 1992).

Although experimental manipulation of predator abundance may lead to changes in plankton abundance, it is less clear that variation in prey abundance in nonexperimental situations is related to predator abundance, after controlling for resource levels. Our results show that, at least in south-central Canadian lakes, algal biomass does vary inversely with zooplankton biomass, after controlling for phosphorus. However, the only apparent effect of piscivorous fish is on the distribution of zooplankton body size. Neither algal nor zooplankton biomass is related to the presence of piscivores in these unmanipulated systems, in contrast with the suggestion of trophic cascade models (Carpenter and Kitchell 1985) or biomanipulation scenarios (Shapiro and Wright 1984).

Our results relating residual variation in chlorophyll concentrations to characteristics of the zooplankton are consistent with several other published studies (summarized in Table 5). In some studies, algal biomass covaries with zooplankton biomass (e.g., this study; Carpenter et al. 1991), while in other cases, zooplankton size is important (Mills and Schiavone 1982; Pace 1984; Carpenter et al. 1991). In all cases, amounts of variance explained are modest. Nonsignificant relationships in the literature could plausibly be due to insufficient statistical power. It seems likely that zooplankton are responsible for some of the among-lake variation in chlorophyll concentrations.

However, while the literature does contain reports that variation in plankton biomass may relate to characteristics of the fish assemblages (in contrast with our results), closer examination shows the evidence to be very thin. Mills and Schiavone (1982), for example, reported differences in zooplankton abundance between lakes with and without piscivores. However, average total phosphorus levels also differed between these two groups of lakes in their data set ($F_{1,11} = 31.3$, $p < 0.001$). When we reanalysed their data and controlled for total phosphorus differences (using ANCOVAs), the differences in plankton abundance between lakes with and without piscivores disappeared (Table 5). Persson et al. (1992) also reported similar differences, but their study suffered from the same difficulty: total phosphorus differed between the two groups of lakes ($F_{1,9} = 8.4$, $p = 0.017$). After controlling for phosphorus, their predator-based relationships also become nonsignificant.

Mazumder (1994) argued that "odd-link" systems (those with abundant planktivorous fish and (or) few large-bodied cladocerans) have more chlorophyll per unit phosphorus than do "even-link" systems (with more abundant large cladocerans). Mazumder's (1994) results suggest that character-

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Table 5. Top-down or predator-controlled relationships: linear relationships between characteristics of a given trophic level and those of its predators, as reported by several authors.

Link	Dependent variable	Independent variable	This study	Mills and Schiavone 1982	Pace 1984	Quirós 1990	Carpenter et al. 1991	Persson et al. 1992
Biomass and abundance relationships								
2–1	Chl *a*	Cladoceran *B*	–	ns[a]			–	
2–1	Chl *a*	Crustacean *B*	–			–[b]		
2–1	Chl *a*	Microzooplanktob *B*	ns					
2–1	Chl *a*	Zooplankton *B*	–	ns[a]	ns		–	ns[a]
3–1	Chl *a*	Planktivore *B*						ns[a]
3–1	Chl *a*	Plantivore *N*		ns[a]		+[b]		
4–1	Chl *a*	Piscivore *B*						(–)[a]
4–1	Chl *a*	Piscivore *N*		ns[a]				
4–1	Chl *a*	Piscivore +/–	ns	ns[a]				(–)[a]
3–2	Zooplankton *B*	Planktivore *B*						ns[a]
3–2	Zooplankton *B*	Planktivore *N*		ns[a]				
4–2	Zooplankton *B*	Piscivore *B*						ns[a]
4–2	Zooplankton *B*	Piscivore *N*		ns[a]				
4–2	Cladoceran *B*	Piscivore +/–	+[c]					
4–2	Microzooplankton *B*	Piscivore +/–	(–)					
4–2	Zooplankton *B*	Piscivore +/–	ns	ns[a]				ns[a]
4–3	Planktivore *B*	Piscivore +/–		(–)[a]				ns[a]
Size relationships								
2–1	Chl *a*	Cladoceran DW	ns	(–)[a]	ns[a], [–][d]		–[e, f]	
2–1	Chl *a*	Zooplankton DW	(–)	–[a]			–[e]	
3–2	Cladoceran DW	Planktivore *N*		ns[a]				
3–2	Zooplankton DW	Planktivore *N*		ns[a]				
4–2	Cladoceran DW	Piscivore *N*		ns[a]				
4–2	Zooplankton DW	Piscivore *N*		ns[a]				
4–2	Cladoceran DW	Piscivore +/–	+	(+)[a]				
4–2	Zooplankton DW	Piscivore +/–	(+)	+[a]				
4–2	Var(Zooplankton DW)	Piscivore +/–	(+)					

Note: In all cases, total phosphorus was included in the model as a covariate in order to hold constant the effect of trophic status. Variables include the logarithms of chlorophyll *a* concentration (Chl *a*) and of the biomass (*B*), abundance (*N*), presence/absence (+/–), and mean individual dry weight (DW) of components of zooplankton or fish assemblages. Zooplankton components include cladocerans, crustaceans, microzooplankton, and total zooplankton, while fish components include planktivorous fish and piscivorous fish. Not all authors measured the same variables; therefore, relationships not reported are left blank. Relationships designated "ns" are those for which $p > 0.20$. Those for which $p < 0.05$ are designated by their sign. The sign of relationships for which $0.05 \leq p \leq 0.20$ is given in parentheses in order to show cases where a more powerful experimental design might have revealed a relationship. Link designates the trophic levels involved, with the dependent variable to the right of the hyphen and with 1 = phytoplankton, 2 = zooplankton, 3 = planktivorous fish, and 4 = piscivorous fish. There is very little evidence that aquatic organisms' biomass is related to that of higher trophic levels, except at the zooplankton–phytoplankton link. There is more evidence that the size structure of plankton assemblages may be influnced by higher trophic levels.

[a]Although the authors did not report this correlation, data presented in the tables and (or) figures permit one to calculate it.

[b]Quirós (1990) reported multiple regressions in which these terms figure. The relationships may be artifacts of the nonlinear relationship between chlorophyll and phosphorus (see text).

[c]This relationship becomes nonsignificant if one controls for the number of multiple comparisons.

[d]Pace (1984) reported a marginally significant relationship using an index of zooplankton community size.

[e]Carpenter et al. (1991) did not designate this result as significant at $p < 0.05$ in their original report, although our reanalysis finds that it is significant.

[f]Mazumder (1994) reported a similar result: lakes and experimental systems with large cladocerans and few planktivorous fish have less chlorophyll than those without large cladocerans. However, his data included mainly manipulated systems.

istics of predator assemblages beyond piscivore presence/absence may be useful in explaining variance in plankton abundance. However, Mazumder's (1994) data came primarily from experimental manipulations; it is uncertain whether they reflect processes in unmanipulated lakes.

Quirós (1990) also reported that the residuals from a linear relationship between log chlorophyll and log phosphorus in a very diverse set of Argentinean lakes are related to both zooplankton and planktivorous fish abundance. However, Quirós (1990) noted that his chlorophyll–phosphorus relationship is, in fact, nonlinear, even though the statistical models postulate a linear relationship. Since zooplankton and planktivore abundance both correlate with phosphorus in Quirós's (1990) data, it is likely that these variables enter into multiple linear regressions due to lack of fit in the linear model. Since Quirós's (1990) paper does not present the original data, we cannot reanalyze them to test whether his relationships entail statistical artefacts.

The present study does not suffer from these artefacts, and we observe no effects of piscivorous fish. Total phosphorus does not differ between the lakes with versus without piscivores ($F_{1,26} = 0.05$, $p = 0.86$), and the chlorophyll–

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phosphorus relationship is linear. With these data, we observe no differences in plankton abundance between lakes with and without piscivores (Table 5).

In a companion study, Wilson (1996) examined a gradient of fish stocking intensity maintained for several years in a set of neighbouring Ontario lakes. Wilson (1996) treated fish stocking as an experimental manipulation of piscivores on spatial and temporal scales (30 whole lakes manipulated for decades) much larger than those used in most experimental studies. Wilson's (1996) results were essentially identical to those we observed here: algal biomass covaried negatively with zooplankton biomass, after controlling for phosphorus. No significant relationships among piscivorous fish stocking rates, planktivorous fish biomass, or plankton biomass were observed. There is no evidence that chlorophyll levels responded to fish stocking in these managed lakes.

Our results concur with the conclusions of a recent review of top-down and biomanipulation studies by DeMelo et al. (1992). Their review showed that few of the 44 food web biomanipulations published between 1961 and 1989 actually observed a change in phytoplankton biomass or species composition. DeMelo et al. (1992) suggested that numerous other factors may mask predation effects: algal grazability, nutrient or climatic fluctuations, direct nutrient additions by fish, dead fish effects, etc.

Why did we observe no effect of piscivores on plankton abundance when at least some experimental studies have shown effects of fish on plankton? Consider the following hypotheses.

(1) Might predator effects be weak in our study lakes, but strong elsewhere? Most of our lakes are on the Canadian Shield, and most are likely to be strongly phosphorus limited. Predator effects might not be expected in strongly phosphorus-limited lakes if phosphorus limitation extended to higher trophic levels (e.g., Sterner and Hessen 1994). It is certainly possible that our lakes are, in some way, atypical. Correlative studies such as ours are never carried out on statistically random samples of lakes. However, our review of the literature showed that other correlative studies conducted elsewhere also failed to detect effects of either planktivorous or piscivorous fish. Further, we found no evidence that the strength of top-down effects is mediated by trophic status, either monotonically, as suggested by McQueen et al. (1986), or polytonically, as suggested by Agustí et al. (1992). In the present study, there was no significant interaction between the presence of piscivorous fish and total phosphorus at the zooplankton or phytoplankton level. Earlier studies that did show an interaction (e.g., Drenner et al. 1989) involved manipulations of two lakes or tanks, as opposed to this study, which examined 28 lakes. However, the range of trophic conditions included in our study was not large, and it is possible that predation effects might be more important in systems more eutrophic than those that we examined. It does seem reasonable to conclude at minimum that, in unperturbed oligo- to meso-trophic lakes, the interactions between the top-down effects of fish predation and trophic status are weak, if they exist at all.

(2) Did our study lack the statistical power to detect piscivore effects? Given the sample sizes in our study, all but a fairly subtle effect of predator presence/ absence (<4–14% of the variance in plankton biomass) could be detected. Estimates of piscivore biomass would have been preferable to piscivore presence/absence. However, as piscivores are spatially and temporally much more variable than are phytoplankton or zooplankton, the sampling required would have been beyond our (and most other academic researchers') resources. Probably because of the difficulty of sampling piscivores, the present study represents the strongest extant test of this hypothesis available (to our knowledge), but a stronger test could, in principle, be devised.

(3) Perhaps all predators are not equal. Some of our lakes were dominated by trout and others by bass, walleye, and perch. Since the modes of feeding of these groups of species differ (Scott and Crossman 1973), it is possible that these species have different effects on the plankton communities. Statistically distinguishing them might reveal stronger effects. Our study did not contain enough lakes in each category of fish composition to permit us to test this possibility.

(4) Perhaps conditions created in experiments are sufficiently different from those in nature such that a real effect exists in experiments, but not in nature. Experiments may use unrealistically high fish densities. Experiments may exclude the natural variability of other factors that could mask predator effects in nonexperimental situations. The temporal and spatial scales of experiments are very different from those of natural lakes, and predation effects may be scale dependent. It is also possible that the effects of piscivorous fish predation are not strong enough to be observed two to three trophic levels lower. Most experimental studies that have demonstrated effects of fish predation have manipulated plankivorous fish, eliminating one trophic level. In our view, the (untested) explanation most consistent with the bulk of existing data is that strong effects of fish predation are primarily a consequence of conditions that exist in experiments. In most natural situations, the predation effects are simply too weak to be of consequence.

Our study has an interesting philosophical implication. During the eutrophication debate of the 1960's and 1970's, the problem was to determine what was responsible for the variation of algal biomass among lakes, and through time in particular lakes. Correlations between the variation in plankton abundance among lakes and nutrient levels (e.g., Dillon and Rigler 1974) suggested that nutrients might be important in controlling algal biomass, and subsequently, experiments tested whether the nutrient–algae interaction was direct (e.g., Schindler 1977; Edmondson 1991). These two observations essentailly resolved the eutrophication debate. The trophic cascade hypothesis is similar, proposing that some of the residual variability in chlorophyll–nutrient relationships is related to predator abundance (Carpenter and Kitchell 1985). Yet, in the latter case, a great deal of effort has been spent on (expensive) experimental manipulation (DeMelo et al. 1992), even though little (cheap) correlative evidence of an effect had been found. The order of effort seems backwards. Moreover, the importance of predator effects in lakes is widely cited in the literature, even though the evidence deals with manipulated systems. Experiments show only that, un-

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der the circumstances created in experiments, predators *can* affect plankton abundance. They do not show how important predator effects are in practice, relative to all other factors that affect plankton abundance. In the absence of a correlation showing that variation in algal abundance is related to variation in predator abundance, the justification for experimental manipulation of predators is much less apparent.

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Habitat selection and clustering of a pelagic fish: effects of topography and bathymetry on species dynamics

Christos D. Maravelias

Abstract: Two dynamic aspects of the ecology of pelagic fish, distribution and abundance, have been linked to topographic, bathymetric, and biotic factors. The two-stage generalized additive modelling (GAM) approach undertaken in the present study offered biological interpretations of presence/absence of a pelagic fish species as distinguished from abundance (if present) in relation to various abiotic and biotic factors. The data were collected during the ICES coordinated Atlantic herring (*Clupea harengus*) acoustic surveys (ICES Division IVa) of July 1992, 1994, and 1995 in the northern North Sea. The depth of the water column, the seabed substrate, and zooplankton biomass appeared to be significant factors modulating presence and relative abundance of a pelagic species within the northern North Sea. Results indicated that habitats with the higher probability of finding herring present were those located in shallower waters having a gravel/sand type of seabed that also carried the highest zooplankton abundances. Species clustering was found to be preferentially higher in these habitats. Notwithstanding their pelagic nature, herring exhibit preferences for areas with specific bathymetric, substratum, and zooplanktonic conditions. These preferences are believed to be linked to the oceanography of the North Sea ecosystem.

Résumé : Deux aspects dynamiques de l'écologie des poissons pélagiques, la distribution et l'abondance, ont été reliés à des facteurs topographiques, bathymétriques et biotiques. La méthode utilisant un modèle additif généralisé à deux degrés appliquée dans la présente étude a offert des interprétations biologiques de la présence ou de l'absence d'une espèce de poisson pélagique, par opposition à l'abondance de cette espèce (si elle est présente), en rapport avec divers facteurs abiotiques et biotiques. Les données ont été recueillies durant les relevés acoustiques du hareng atlantique (*Clupea harengus*) coordonnés par le CIEM (Division IVa du CIEM) réalisés en juillet 1992, 1994 et 1995 dans le nord de la mer du Nord. On a observé que la profondeur de la colonne d'eau, le substrat du fond marin et la biomasse zooplanctonique étaient des facteurs qui déterminaient de façon importante la présence et l'abondance relative de l'espèce pélagique qu'est le hareng dans cette zone. Les résultats ont indiqué que les habitats le plus susceptibles d'abriter le hareng étaient les eaux peu profondes dont le fond était graveleux ou sableux et qui connaissaient les plus fortes abondances de zooplancton. C'est dans ces habitats qu'on a préférentiellement observé les plus importants regroupements d'espèces. Malgré sa nature pélagique, le hareng préfère les zones montrant une bathymétrie, un substrat et des conditions zooplanctoniques spécifiques. On croit que ces préférences sont liées à l'océanographie de l'écosystème de la mer du Nord.

[Traduit par la Rédaction]

Introduction

Fisheries management has not always been successful in maintaining fish yields and conserving stocks. Evidence is mounting that our information concerning the biology and ecology of many fish species may be insufficient to establish reliable estimates of yields. It is now clear that the role of the environment cannot be excluded from fisheries management and that oceanographic data may contribute useful and necessary information. Fisheries scientists have long investigated changes in the marine ecosystem in relation to environmental changes (Hardy 1936; Cushing 1975; Sutcliffe et al. 1977; Raid 1989; Mann 1993; and references therein). As a result, significant correlations between fluctuations in abundance and (or) distribution of commercially important fish stocks and environmental and biotic factors have been found.

In the present study, two dynamic aspects of the ecology of a pelagic species, distribution and relative abundance, were examined for evidence of correlation with specific water depth zones, substrate types, and prey availability in order to learn about the processes that may modulate fish presence and abundance in the North Sea using the North Sea Atlantic herring (*Clupea harengus*) population as an example.

Data collected during acoustic surveys carried out in July 1992, 1994, and 1995 in the northern North Sea (Orkney–Shetland area, ICES Division IVa, Fig. 1) were examined. The analysis of three years of consecutive surveys enabled the investigation of whether the distribution and abundance of a highly migratory pelagic species are similar between

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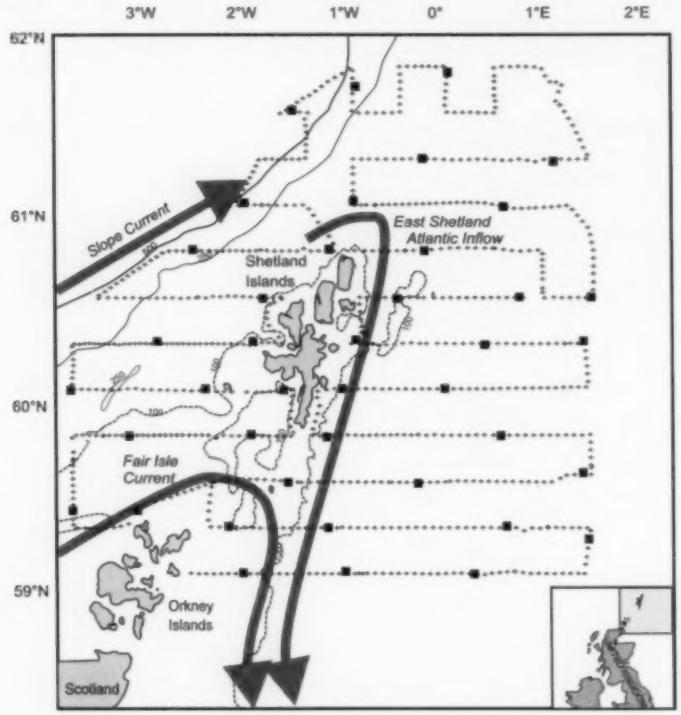
Fig. 1. Bottom topography (m) of the study area, northern North Sea (ICES Division IVa). Arrows indicate main currents and water movements in the area, and squares indicate trawling sites and zooplankton hauls. The pluses indicate the survey track of the FRV *Scotia* during the 1992 survey.



years and whether the process of habitat selection and species clustering might be affected by biotic and abiotic (e.g., water depth, seabed substrate) factors in a similar manner across the study years.

Acoustic surveys are able to give quasi-synoptic data on the distribution of fish biomass over a wide area and are not dependent on commercial catch statistics (MacLennan and Simmonds 1992). Importantly, acoustic surveys cover areas with low fish abundance (that are not commercially exploited) as well as areas with high fish abundance. As a result, studies based on such data are not subject to problems of misreporting bias and poor spatial and temporal resolution. The simultaneous collection of a wide range of ancillary variables, i.e., biotic (e.g., zooplankton), hydrographic (e.g., water depth), substrate type (e.g., RoxAnn), during acoustic surveys offers a platform of opportunity for studying the relationship between population dynamics and environment.

In the past, most of the wildlife–habitat correlations that have been demonstrated involved a single environmental parameter (e.g., temperature) and a biological parameter (e.g., abundance of a given species) and had often ignored the nonlinear and nonmonotonic nature of such a relationship (Mann 1993). The current analysis was conducted using a nonparametric regression technique, called the generalized additive model (GAM), that offers advantages over conventional regressive methods because it is not dependent on specific functional relationships (e.g., linearity) and it is less restrictive in its assumptions about the underlying statistical distribution of the data. In a GAM the covariates are assumed to affect the dependent variable, in this case, fish presence and abundance, through additive and unrestrictive smooth functions (Hastie and Tibshirani 1990).

The herring is a highly mobile pelagic schooling species and is the only marine clupeoid with demersal eggs laid in areas of gravel on the seabed (batch spawning is the most common mode of reproduction for the herring species; Blaxter 1990). Herring are believed to be rather conservative with respect to their spawning grounds, which are usually located in high-energy environments either nearshore or in tidally active areas. It has been suggested that herring migrate from offshore feeding grounds to nearshore holding areas one to several months in advance of spawning to finally disperse to the ultimate spawning location a few days to a few weeks prior to spawning (Haegele and Schweigert 1985). The species starts feeding in April in areas that contain a high abundance of *Calanus finmarchicus* or euphausids. *Calanus* is the principal food organism for herring (Parrish and Saville 1965). Herring feeding continues until July, when they stop feeding and start aggregating in prespawning schools. These schools gradually move in the direction of the various spawning grounds that are located, in the case of the studied area, near Shetland–Orkney islands. Heath et al. (1985) showed that east of Orkney, spawning sites are closely related to hydrographic features, especially the Fair Isle Current.

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Materials and methods

Survey data

The herring abundance data were collected during the coordinated herring acoustic surveys conducted by the Marine Laboratory of the Scottish Office of Agriculture, Environment and Fisheries (SOAEFD) in the northern North Sea (i.e., the Orkney–Shetland Islands area, International Council for the Exploration of the Sea (ICES) Division IVa) under the auspices of ICES. The survey design and conduct of the surveys are well established and are described in detail in Simmonds et al. (1995). Water depth was collected as part of the acoustic data during these surveys.

During the 1995 survey, vertical plankton samples were also taken using a standard plankton net (250-μm mesh size, 1 m in diameter) from the upper 60 m of the water column. Samples were fixed and preserved in excess borax-buffered 4% formaldehyde solution and then sorted. Species were later identified to species, counted, and converted to dry weights, i.e., milligrams dry weight biomass per cubic metre, for the top 60 m of the water column (for a detailed description, see Hay 1995). For the purposes of the present study, the small crustacean category was used. This category was dominated (99%) by calanoid copepods (mainly *C. finmarchicus*) at various stages of development. *Calanus* is known to be the main prey of herring and comprises more than 70% of the entire zooplankton in the northern North Sea during June–July (Fransz et al. 1991).

Information with respect to seabed substrate was provided for all three years using a commercially available acoustic substrate classification system (RoxAnn, Marine Microsystems, Aberdeen). It is designed to be connected to the raw return signal from any type of echosounder. In the present studies, it was connected to one of the quadrants of a SIMRAD EK500 38-kHz split-beam echosounder. The raw signal is processed in hardware by the RoxAnn system. In simple terms, two parameters are extracted from the return signal. The first (E1) is the gated tail of the first seabed echo. It is believed to represent seabed "roughness". Any roughness on the seabed will tend to scatter the sound more generally, and therefore, some will return to the transducer and be picked up as part of the tail of the echo. It is believed that the rougher the seabed, the stronger this tail becomes. The second parameter (E2) is the gated second seabed echo. The strength of the first part of the seabed echo is modulated by seabed "hardness". The harder the seabed, the stronger the echo, and hence the stronger the second echo. In other words, the harder the seabed, the more sound is reflected back and forth between the seabed and the surface and so contributing to the second echo.

These two parameters, representing roughness and hardness of the seabed, can be used to define the type of substrate. During the surveys, the RoxAnn system was set to gather data at 15-s intervals. E1 and E2 values were represented as analogue values on two outputs of the RoxAnn instrument. These were displayed using MacSea software, and E1 and E2 values were assigned to a user-definable colored box set providing a real-time indication of the cruise track and of variation in the seabed substrate. More specific details of the theoretical basis of RoxAnn are given in Chivers et al. (1990); a field evaluation of RoxAnn is presented in Schlagintweit (1993).

Exploratory data analysis (EDA)

Herring abundance and water depth data were available at 15-min intervals (every 2.5 nautical miles). Zooplankton biomass was available at stations, hence covering a small subset of the total fish abundance data locations. Kriging, which explicitly accounted for the presence of spatial autocorrelation, was used to interpolate onto most of the abundance data locations (specific details of the kriging technique as applied in the present study are given in Maravelias 1997). The RoxAnn system recorded four values of E1 and E2 every minute (i.e., 15-s intervals). Averaging was undertaken to obtain single values of E1 and E2 for each herring density measurement. The values of E1 and E2 for each 2.5 nautical miles of survey track were determined by overlaying the cruise track on the coordinates of the recorded variables. Values of E1 and E2 that were recorded from minute 1 (in time) up to and including minute 15 were averaged and assigned to the first quarter-hour value of density, i.e., 0:15:00. Values of E1 and E2 that were recorded from minute 16 up to and including minute 30 were averaged and assigned to the second quarter-hour value of herring density, i.e., 0:30:00, in a analogous way. The same procedure was applied to the rest of the values, which were then included in the analysis. The bottom classifications obtained were fairly consistent from survey to survey.

Fisheries acoustic surveys perform continuous sampling along the cruise track. As a result, the data are serially autocorrelated. In an attempt to handle the spatial autocorrelation of the data, I used the information obtained from a separate 4-year geostatistical study (1992–1995) of the herring population in the northern North Sea (Maravelias 1997). Herring have been found to remain spatially autocorrelated up to 7–9 nautical miles (Maravelias et al. 1996; Maravelias 1997). Binning the data in hourly values (every 10 nautical miles) diminishes any problem due to spatial autocorrelation of the data. I had the option of relating fish abundance to the variables examined using only these hourly values. However, it was preferred to use the full abundance data set, which was an order of magnitude larger, in order to avoid the loss of spatial resolution of the data. I justify doing this by the similar results obtained when the same GAM analysis was performed on the above-mentioned subset of the abundance data (i.e., binned in hourly values). There was no significant change either in the shape of the relationships (i.e., GAM plots) or in the significance values of the models.

Based on the Marine Laboratory's grab sampling database and ground truthing, E2 values lower than 0.6 V were known to represent soft sediment types, i.e., mud and silt, E2 values higher than 0.6 V and lower than 1.2 V were characteristic of sand and gravel seabed grounds, E2 values higher than 1.2 V and lower than 1.5 V represented stone-covered seabeds, and E2 values higher than 1.5 V reflected rocky seabed substrate. On each of the three surveys, the RoxAnn readings were calibrated based on the classification of the sediments obtained from the grab samples taken.

Scatterplots of all the studied parameters were produced in order to visualize and suggest possible relationships between the variables. The spatial distributions of herring, seabed roughness (RoxAnn E1), seabed hardness (RoxAnn E2), and zooplankton biomass (available only for 1995) for each year were visualized and mapped using SURFER 6.0 (Golden Software Inc.). For the numerical analysis of GAMs, the SPLUS 3.3 software (MathSoft Inc.) was used.

GAMs

One obvious characteristic of acoustic survey data is the large number of zero observations. Data with such a high proportion of zeros are usually difficult to model in one step. Here, I implemented a two-stage model: first the probability of presence of herring, and second the number of herring (abundance as EAI) given that some were observed (Borchers et al. 1997). The general form of the GAMs is given by (Hastie and Tibshirani 1990)

$$E[y] = g^{-1}(\beta_0 + \sum_k S_k(x_k))$$

where $E[y]$ is the expected value E of the response of a random variable y (here, herring abundance), $g()$ is the link function defining the relationship between the response and the additive predictor $\beta_0 + \Sigma_k S_k(x_k)$, β_0 is an intercept term, x_k is the value of the kth

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spatial covariate, and $S_k()$ represents smooth functions of the k covariates.

Appropriate link functions and error distributions were chosen on the basis of residual plots (Hastie and Tibshirani 1986, 1990; Swartzman et al. 1992; Borchers et al. 1997). A GAM with logit link, binomial error structure was implemented in the first stage of modelling. The binomial family uses the logit link function defined by

$$g(p) = \text{logit}(p) = \log\left(\frac{p}{1-p}\right)$$

where p is the probability of an event (i.e., detection of herring) occurring (Chambers and Hastie 1992). The parameter p corresponds to the mean response of a binary (0–1) variable (i.e., here, presence/absence). The generalized additive logistic model for the first stage of modelling was finally (Venables and Ripley 1994)

$$\text{logit}(p) = \alpha + \sum_{j=1}^{p} f_j(X_j)$$

In the second stage, a GAM with a log link function and Gaussian error distribution was found to be adequate for the data modelled here. The backfitting algorithm (Hastie and Tibshirani 1990) cycles through the covariates, improving the overall smooth at each iteration until the deviance (the measure used for fit of the model to the data) no longer decreases. The deviance, or likelihood ratio statistic, plays the role of the residual sum of squares for generalized models (Hastie and Tibshirani 1990; Venables and Ripley 1994).

In GAMs, for a given combination of error distribution and link function, the model selection involves both the choice of terms to involve in the model and how smooth (i.e., the degree of smoothing of $S_k()$) they should be. The least squares estimate of the multiple linear regression is replaced by a local smoother in GAMs; here, the cubic spline smoother s (Hamming 1973) was used. The degree of smoothing performed by the smoother $S_k()$ was determined on the basis of the observed data sets. The available covariates examined here were RoxAnn E1 (seabed roughness), RoxAnn E2 (seabed hardness), water depth, and zooplankton biomass (1995 only). All available variables and their first-order interactions were initially included in the model. Backward stepwise elimination was used to select a set of significant covariates. To evaluate these differences and compare the models, approximate F tests based on the approximate degrees of freedom and the corresponding percentage point of the F distribution were computed, as suggested by Hastie and Tibshirani 1990 (for an application, also see Swartzman et al. 1992). Analysis of deviance compared models by analyzing changes in deviances relative to the changes in degrees of freedom. Estimation of the variability of the trends was performed using a parametric bootstrap with two levels (one generating presence/absence data and the other generating numbers given presence). A more detailed description of the bootstrap is given elsewhere (Swartzman et al. 1992; Borchers et al. 1997; Maravelias 1997), and I refer the reader there for more information.

Results and discussion

EDA

The highest fish abundances were found in areas characterized by a seabed of gravel and sand (0.4 V < E1 < 0.7 V and 0.6 V < E2 < 1.2 V) of intermediate bottom depths, i.e., 70–150 m, while deeper waters carried low fish biomass (Fig. 2). In 1995 the larger fish aggregations were also observed in areas that carried high zooplankton biomass (>50 mg/m^3). The spatial distribution maps of the studied variables are given in Figs. 3–5.

Table 1. Significance values (p levels) for all GAM covariates and their interactions.

	Two-stage modelling		
Covariate	1992	1994	1995
Presence/absence			
Seabed roughness	0.007	0.04	0.001
Seabed hardness	0.001	0.04	0.001
Bottom depth	0.001	0.005	0.001
Zooplankton biomass	na	na	0.001
Bottom depth – zooplankton biomass interaction	na	na	0.001
Herring density given presence			
Seabed roughness	ns	ns	ns
Seabed hardness	0.001	0.001	0.02
Bottom depth	0.04	0.002	0.04
Zooplankton biomass	na	na	0.04
Bottom depth – zooplankton biomass interaction	na	na	ns

Note: Level of significance was set to 0.05. ns, nonsignificant; na, not available.

GAMs

To better understand the effect of each of the explanatory variables included in the GAMs, I examine the fitted contribution of each variable to total herring abundance plotted against the value of the variable. The 95% confidence intervals are also plotted around the best fitting smooths for the main effects. Interaction effects are shown as perspective plots without error bounds. The y-axis reflects the relative importance of each covariate of the model; for the interaction effects, this is presented on the z-axis. Finally, the x-axis for the single covariate effect plots includes a so called "rug", which shows the density of points for each covariate included in the model. It needs to be emphasized that the effect of each variable is the conditional effect, i.e., the effect that this variable has, given that the other variables are included in the model. The significance values (p levels) of GAM covariates and their interactions for all years and stages of the analysis are given in Table 1.

The results of the two-stage GAM modelling are shown in Figs. 6*a*, 7*a*, and 8*a* for the first stage and in Figs. 6*b*, 7*b*, and 8*b* for the second stage. In the first stage, the presence/absence of prespawning herring was modelled (i.e., the probability of detecting fish present). The bottom depth, seabed hardness, and seabed roughness were found to be highly significant covariates (in this order of significance) in all three years. For 1995, zooplankton biomass was also highly significant either as a main effect or through its interaction with bottom depth.

In the second stage, the mean abundance of fish was modelled given presence. Seabed hardness, bottom depth, and zooplankton biomass (1995 only) were significant explanatory variables. An obvious feature of the GAM plots of this stage is the slight change in the shapes of the smooths (Figs. 6*b*, 7*b*, and 8*b*) compared with the ones already examined (Figs. 6*a* and 8*a*). This is due to the fact that it was the herring density that was modelled here conditioned on pres-

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Fig. 2. Scatterplots of (*a*) 1992, (*b*) 1994, and (*c*) 1995 herring EAI against seabed roughness (RoxAnn E1), seabed hardness (RoxAnn E2), water depth, and zooplankton biomass.

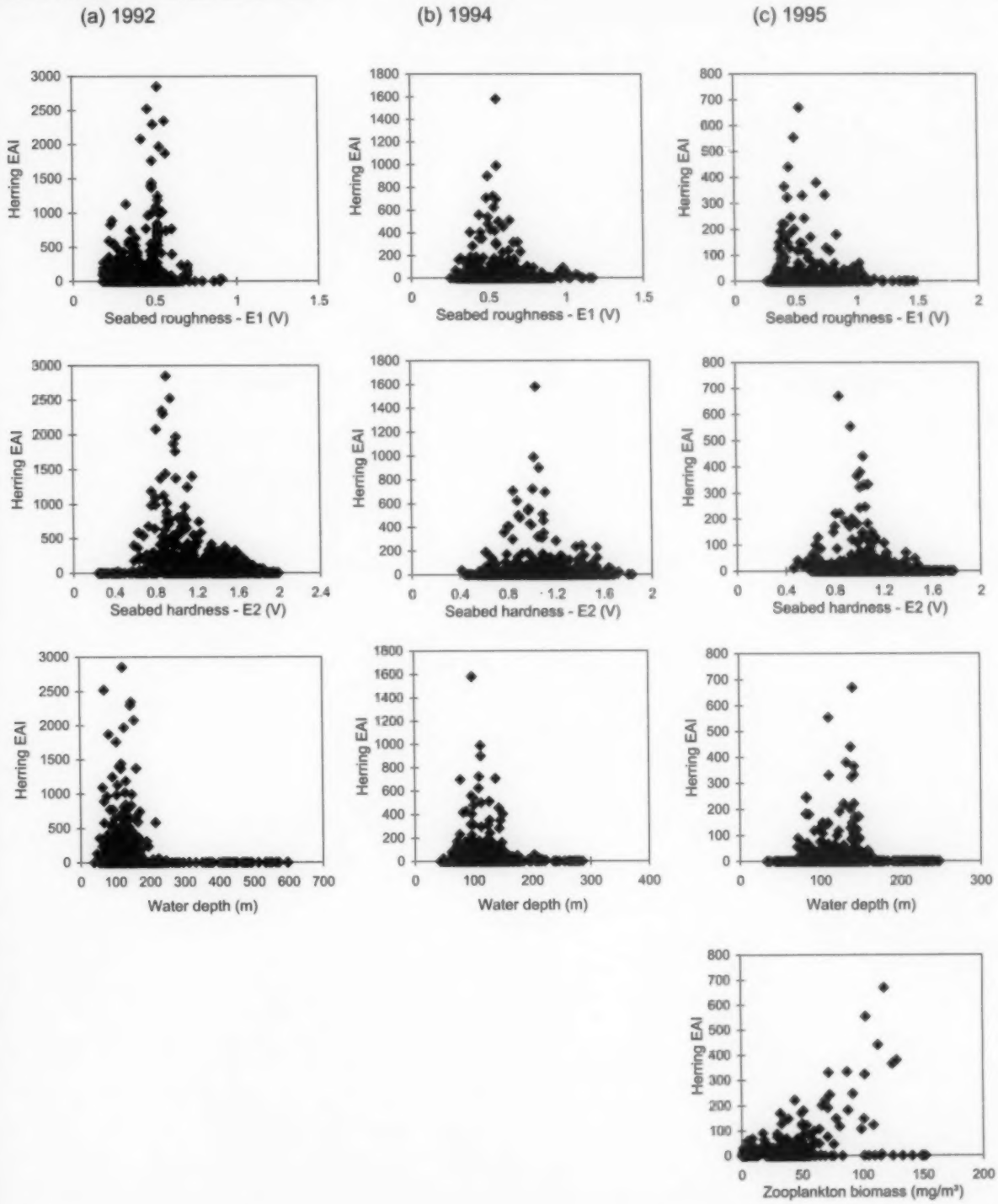

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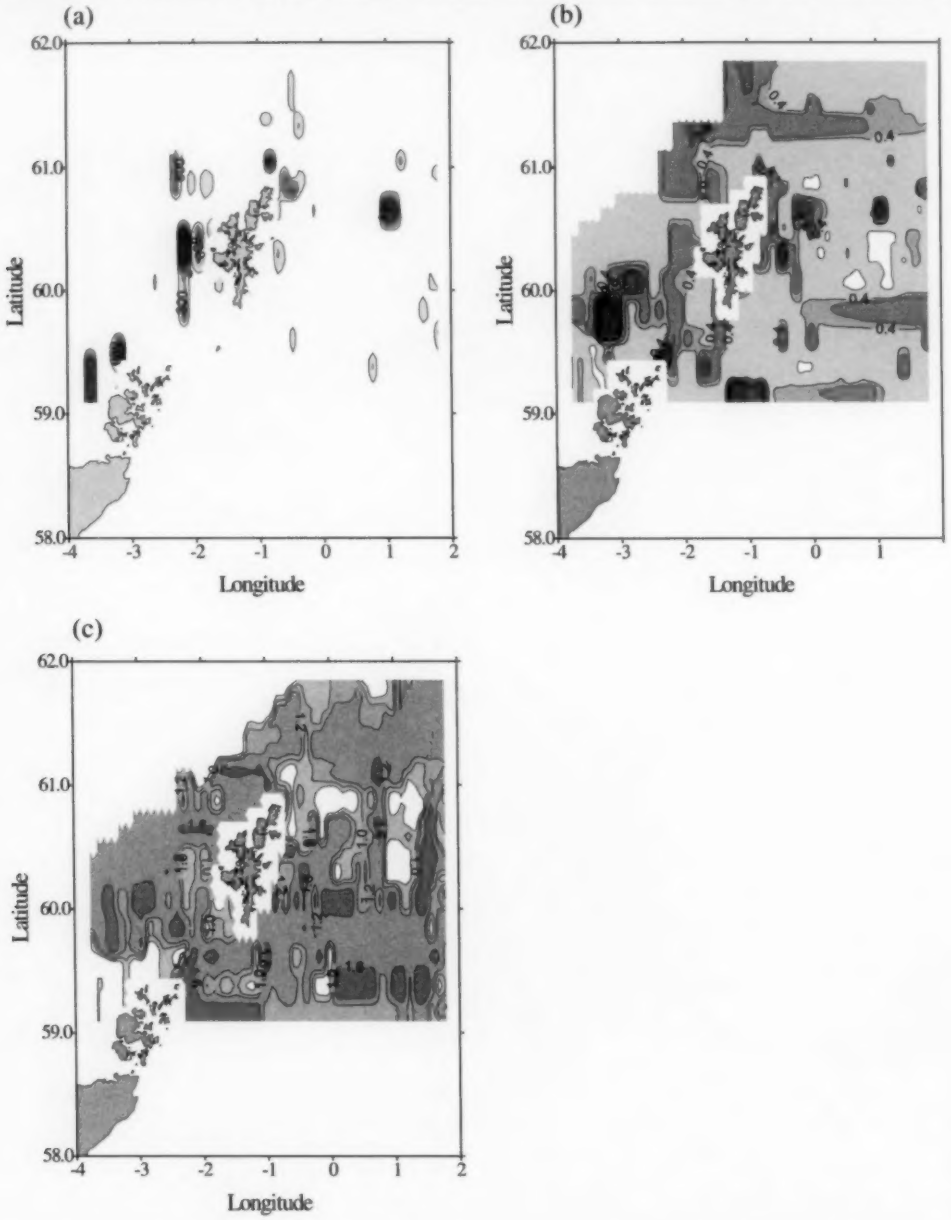
Fig. 3. Spatial distribution of (*a*) herring, (*b*) seabed roughness (RoxAnn E1) (V), and (*c*) seabed hardness (RoxAnn E2) (V) for 1992.



ence. Therefore, the zero observations were not considered in the models and thus did not mask any herring–covariate relationship. An interesting observation of this second stage is that the seabed roughness ceased to be a significant factor in all three years. For 1995, this also applied to the zooplankton – bottom depth interaction.

The prespawning herring in the northern North Sea showed a distinct habitat preference for a gravel/sand type of seabed. The substrate hardness and roughness relationships with herring abundance were found to be significant, and a distinct preference for E2 values between 0.6 and 1.2 V and E1 values lower than 0.8 V was observed throughout the three years (Figs. 6–8). Based on the extensive ground truthing and grab sampling database, these values are known to characterize gravel/sand type seabeds. Results from the two-stage modelling analysis revealed that these areas had the highest probability of having herring present. Moreover, by modelling the numbers of fish given presence, it was found that the largest herring aggregations also showed preference for gravel/sand substrates (E2). From these results, it is clear

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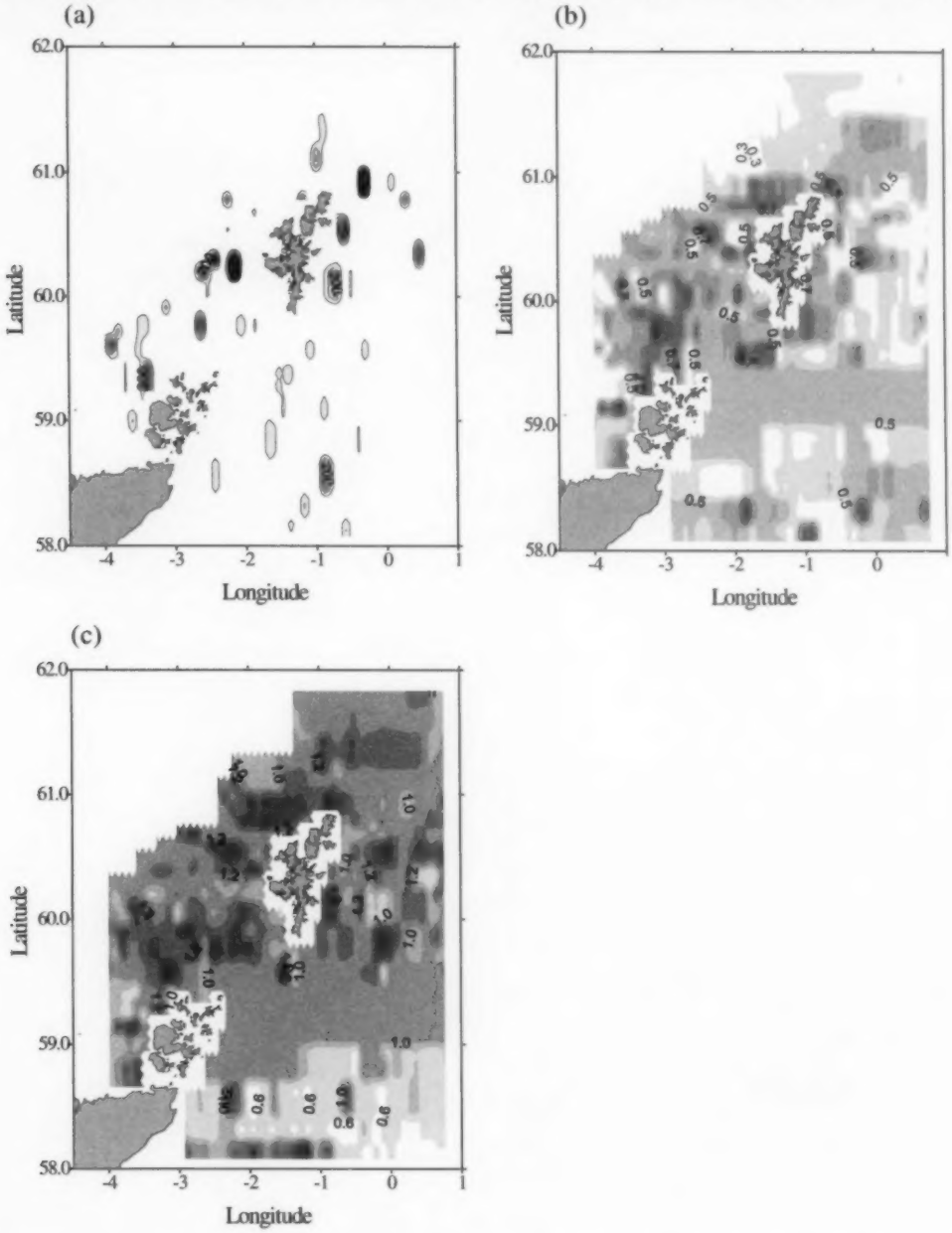
Fig. 4. Spatial distribution of (*a*) herring, (*b*) seabed roughness (RoxAnn E1) (V), and (*c*) seabed hardness (RoxAnn E2) (V) for 1994.



that the fish habitat–substrate preferences were genuine and not simple artifacts of the large number of zero observations encountered during the surveys. These results are in agreement with those reported in previous studies. In the studied area, herring are expected to spawn in August–September, 1–2 months after the surveys are conducted. Herring spawning has been found to be restricted to areas of gravel (Parrish and Saville 1965; Haegele and Schweigert 1985), and the species typically congregates near their spawning grounds for several weeks to months prior to spawning (Haegele and Schweigert 1985). The present observations indicate that this is likely to be true and may explain why a pelagic species might be distributed in relation to seabed substrate.

During the surveys, herring were found mostly in water with the seabed deeper than 70 m, with echo traces being found in waters with depths up to 250 m (Simmonds et al. 1993, 1995). Direct observations made during the surveys indicated that the 200-m isobath, lying alongside the shelf

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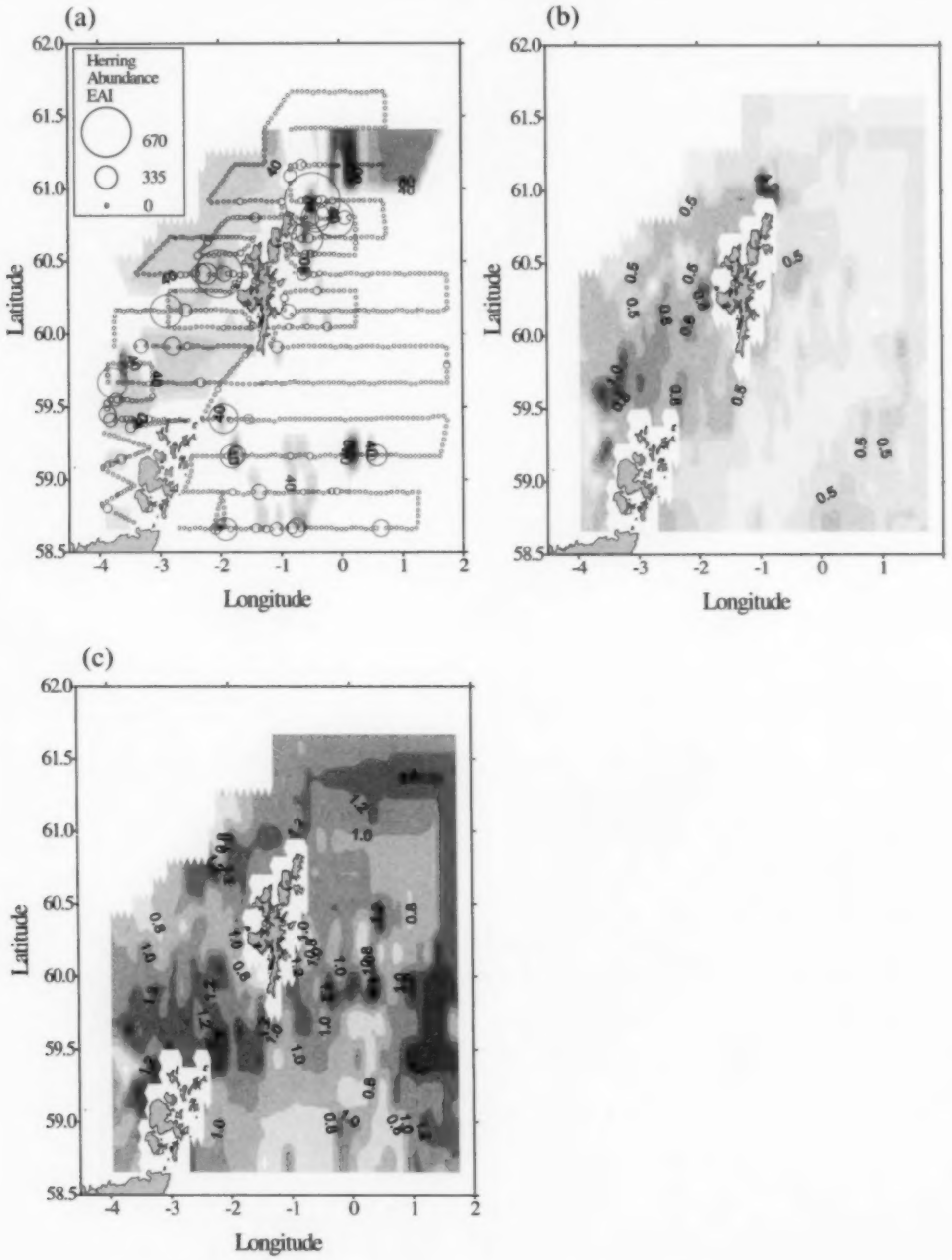
Fig. 5. (*a*) Zooplankton biomass given with a proportional representation of the herring data (upper left) (radius of circles is proportional to herring EAI) and spatial distribution of (*b*) seabed roughness (RoxAnn E1) (V) and (*c*) seabed hardness (RoxAnn E2) (V) for 1995.



edge, limited the distribution of herring to the west. In the present study, bottom depth was found to have both a direct main effect and an interactive effect (through its interaction with zooplankton biomass) on herring abundance (Figs. 6–8). It has been suggested that water depth is a limiting factor that restricts herring distribution in specific depth ranges (Blaxter and Holliday 1963; Blaxter and Hunter 1982; Simmonds et al. 1993). The present results are highly consistent with those reported in previous studies. In all three years, deeper waters had the lowest probability of herring encounter whereas shallower waters (<150 m) carried the higher probability of finding herring present. Furthermore, it was

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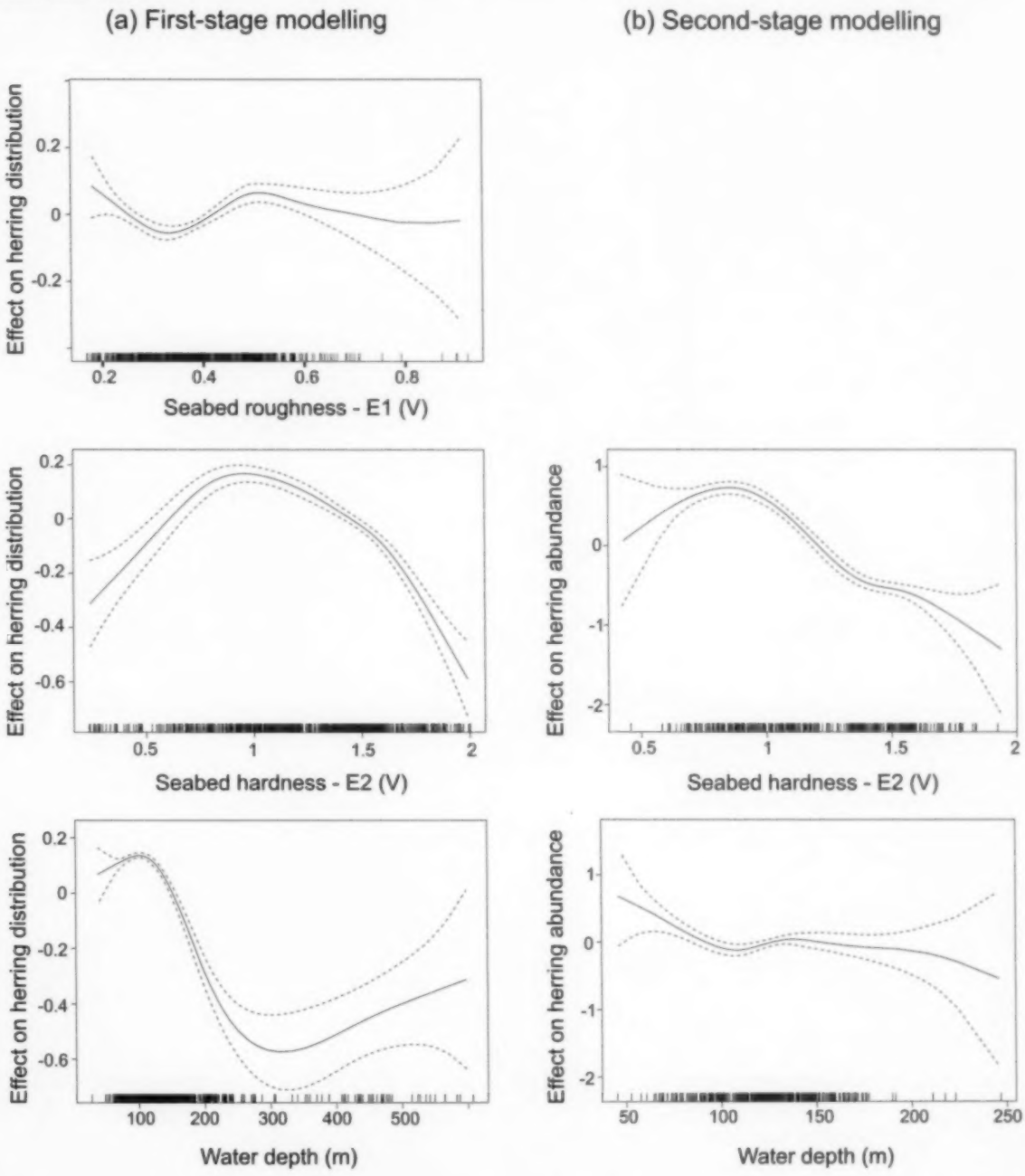
Fig. 6. Results of GAM regression for 1992 (*a*) herring presence/absence and (*b*) herring abundance (log) given presence as a function of seabed roughness (RoxAnn E1), seabed hardness (RoxAnn E2), and water depth. Broken lines represent 2-SE ranges around the covariate main effects.



found that the highest herring abundances were in these shallower (<150 m) waters and that deeper waters were carrying only low herring biomass. Herring during midsummer in the northern North Sea start aggregating in prespawning schools. These schools gradually move in the direction of the various spawning grounds near the Shetland–Orkney Islands. Therefore, it is possible that water depth might modulate both habitat selection and species clustering in these specific areas. Parrish and Saville (1965) also suggested that water depth and the nature of the substratum

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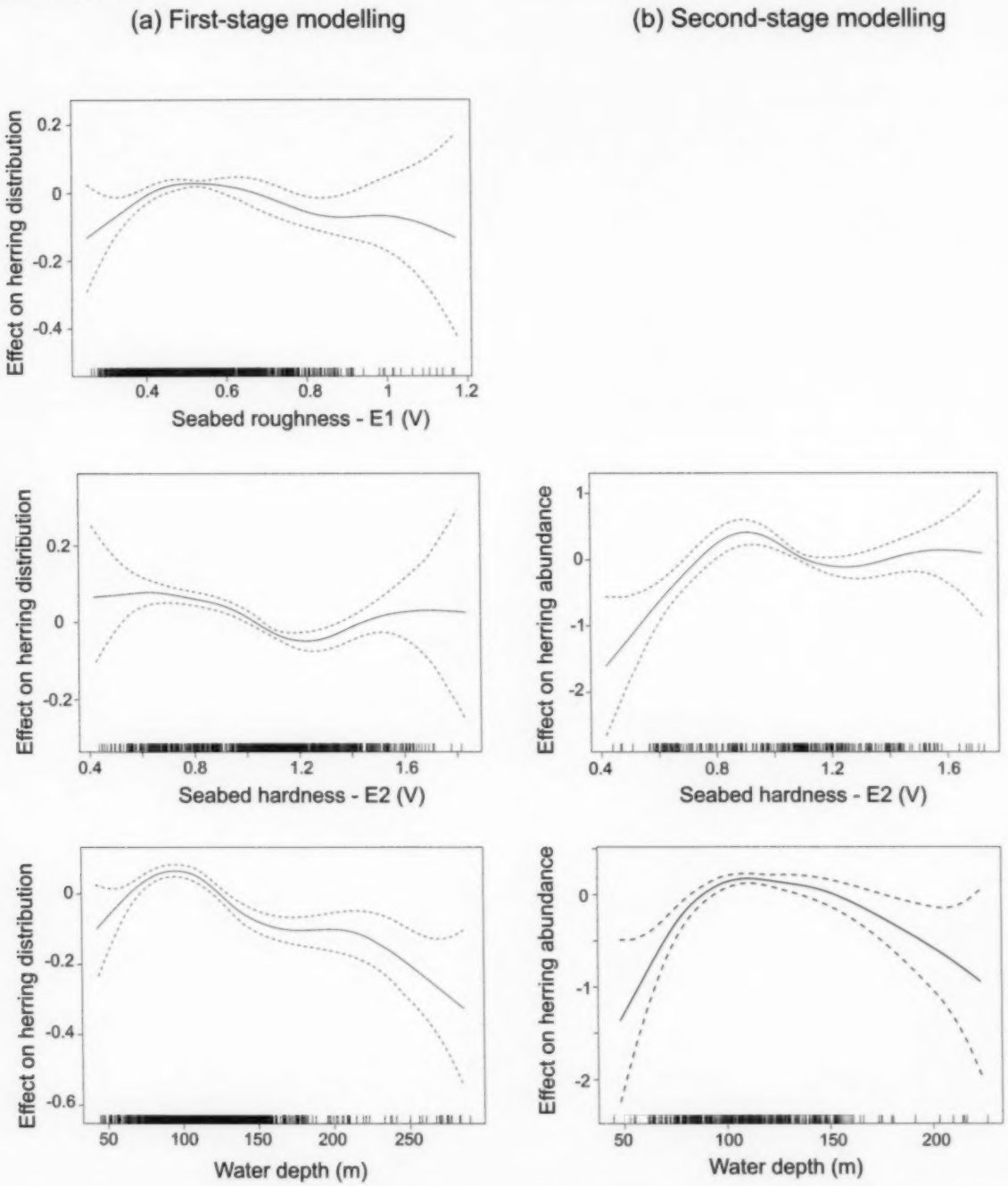
Fig. 7. Results of GAM regression for 1994 (*a*) herring presence/absence and (*b*) herring abundance (log) given presence as a function of seabed roughness (RoxAnn E1), seabed hardness (RoxAnn E2), and water depth. Broken lines represent 2-SE ranges around the covariate main effects.



were the major factors governing the selection of spawning sites.

Many pelagic fish aggregate on patches of food (zooplankton) and disperse in small shoals when the food patch has been grazed down. Jakobsson (1978) described the distribution of Atlanto–Scandian herring in relation to zooplankton distribution, which is the main food for herring. He showed that herring were usually found at the edges of higher zooplankton density areas and within higher zooplankton standing crop areas. This was also observed in the

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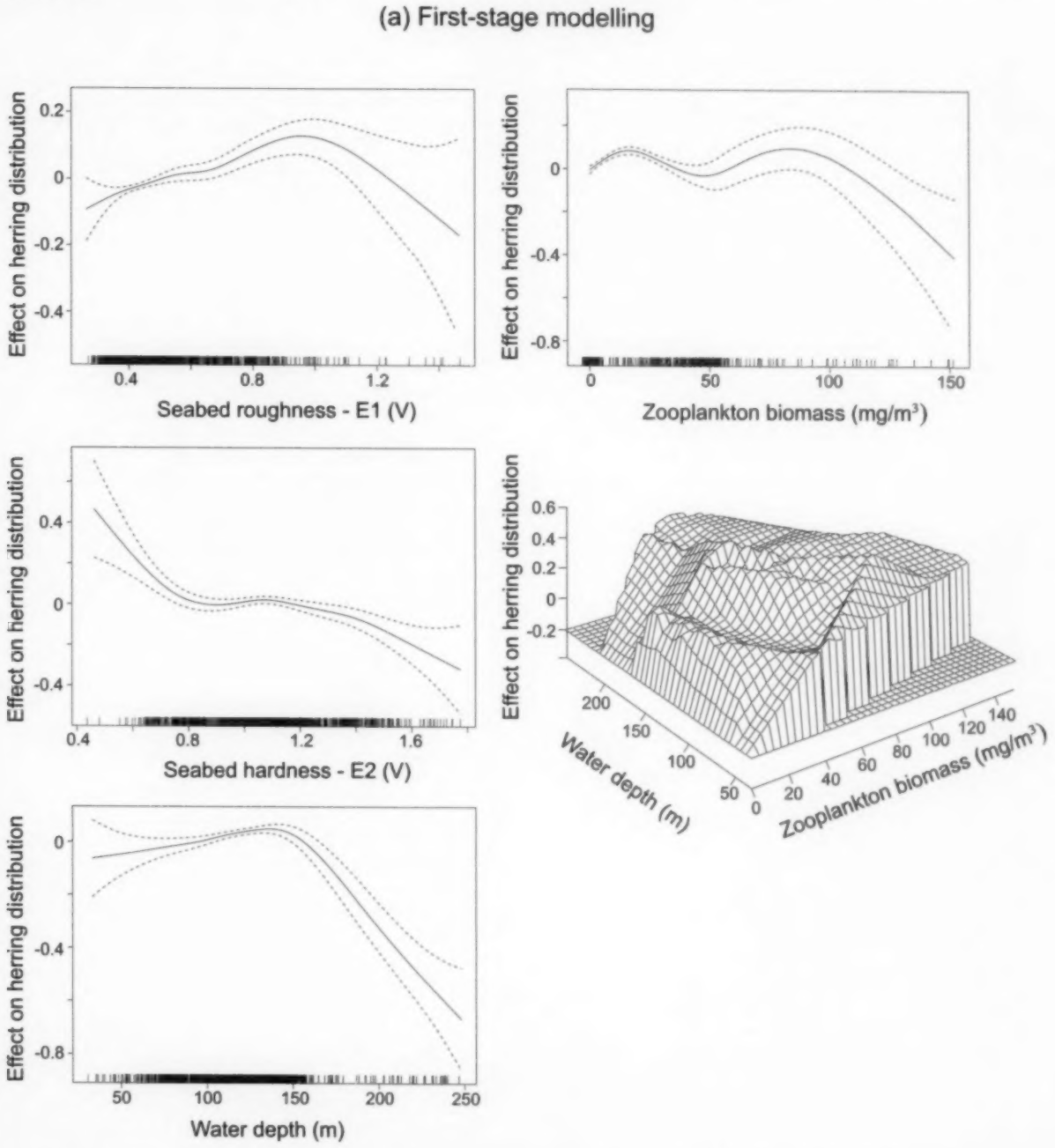
Fig. 8. Results of GAM regression for 1995 (*a*) herring presence/absence and (*b*) herring abundance (log) given presence as a function of seabed roughness (RoxAnn E1), seabed hardness (RoxAnn E2), water depth, zooplankton biomass, and the interaction of water depth with zooplankton biomass. Broken lines represent 2-SE ranges around the covariate main effects. (Figure 8 is concluded on the next page.)



present study. In 1995, zooplankton biomass had a significant effect on species distributional abundance, both directly as a main effect and indirectly through its interactive effect with water column depth (Fig. 8). Zooplankton biomass appeared to be an important factor that might modulate the prespawning distribution (i.e., presence) and relative abundance of a pelagic fish species. It was revealed that herring presence tended to be confined to zooplankton-rich habitats. A closer examination of the positive herring densities (i.e., without the zero value observations that comprised 80.7% of

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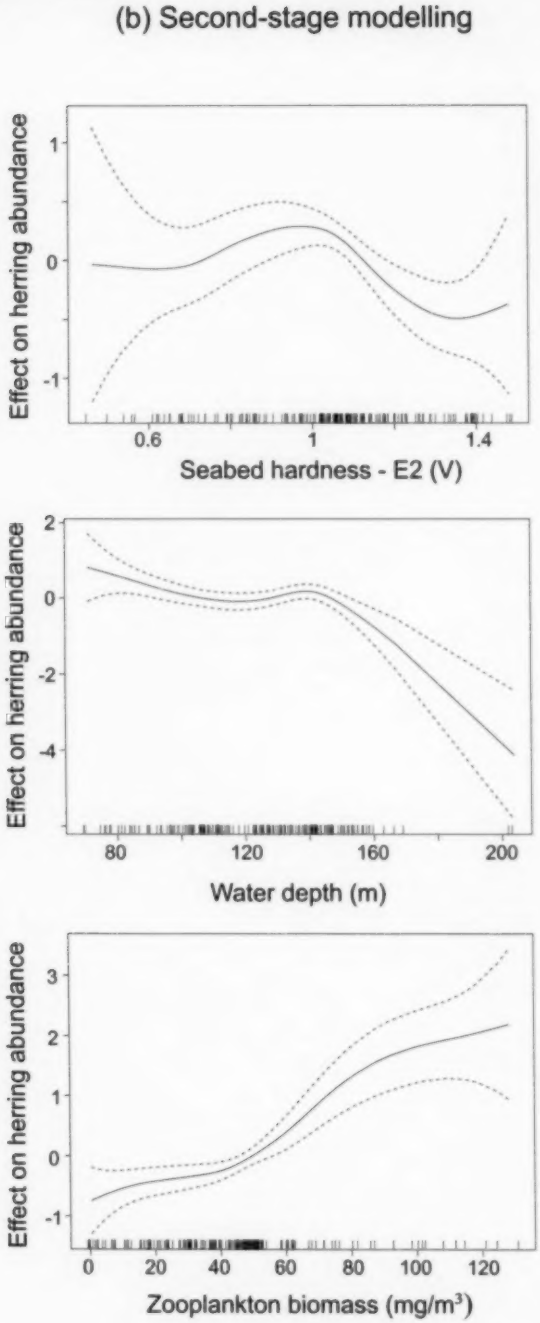
Fig. 8 (*concluded*).



the 1995 data set) also confirmed that the average herring abundances were highest in waters with high zooplankton biomass. A remarkable coexistence of the higher herring abundances with the dense zooplankton patches was also observed. Herring clusters appeared to be located either directly on the plankton patches or at their edges. In the first case, it is reasonable to suggest that herring were in the process of grazing down the dense zooplankton concentrations. In the second case, herring may have still been feeding in the edges of the patch. This infers that zooplankton (i.e., food) availability is likely to govern habitat choice and clustering of a pelagic fish species within an area.

In the marine ecosystem the bottom topography of an area is closely related to its hydrography. The northwestern North Sea (i.e., Orkney–Shetland Islands area) is a hydrographically dynamic area that experienced the "great salinity anomaly" in the 1970's (Svendsen et al. 1991). The main feature is the Slope Current, which is responsible for the input of Atlantic water into the northern North Sea (Turrell 1992). The inflow of Atlantic water into the North Sea has profound implications for the circulation and ecology of this shallow shelf area. This inflow provides a significant input of warmer, nutrient-rich water, bringing in oceanic planktonic species as well as fish larvae otherwise lost from the shelf seas into the warm waters further offshore (Turrell 1992). Nutrients that are brought to the surface by turbulence as the water velocity increases over a shelf or bank can be utilized by the phytoplankton, resulting in a shelf-break front of high primary productivity. Hence, mixing results in elevated surface nutrient concentrations, high primary production, and increased numbers of zooplankton. The highest densities of zooplankton occur in the areas of moderate mixing, adjacent to the path of the strong currents.

In the northern North Sea ecosystem during summer, *C. finmarchicus* emigrate into the deeper water layers in July and August where they will later hibernate; these are waters beyond the shelf edge. At the same time, herring schools are believed to be feeding while moving towards their spawning grounds (Corten and van de Kamp 1992). In any area, soft bottoms are typical of stagnant water (stratified), intermediate bottoms (i.e., gravel) are typical of transition and boundary zones, and very hard bottoms are typical of areas with strong currents. In the present study, herring were found to avoid the areas with high current speeds. Instead, they were distributed in the shallower areas adjacent to the shelf break (i.e., transition zones between frontal and stratified waters). A reasonable scenario would suggest that in these areas, herring were benefiting from the higher food availability of the adjacent waters while retaining themselves in more favorable habitat conditions (i.e., gravel seabeds in shallower waters). Species preferential clustering in these areas could also be attributed to the poorer visibility of these areas (as herring is mainly a visual feeder) or to the metabolic cost, since they would have to spend too much energy swimming against the current.

Conclusions

Unlike oceanographic factors that may change over time, seabed substrate and bathymetry do not change drastically over a specific area. The present results revealed a robust multiyear relationship between herring dynamics and seabed substrate and bottom depth and provided useful insights into the underlying mechanisms governing habitat choice and species clustering in the northern North Sea in summer. This study, although not directly dealing with spawning, also provided evidence that herring demonstrate topographic and

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bathymetric preferences in the months *prior* to spawning, as well as at spawning time.

Fisheries surveys data are characterized by a large number of zero value observations. Analyzing such data sets entails the risk of a likely masking effect on the underlying spatial dependence of the species on variables examined. The two-stage modelling approach undertaken here was implemented in order to examine two aspects of herring biology separately: distribution and relative abundance. The current analysis had the main advantage of the relationships not being masked by the large number of zero value observations (i.e., conditioned on presence).

Changes in the marine climate may have strong influences on oceanic fish populations. The idea behind fisheries oceanography studies, such as the current one, is that a thorough understanding of the fish distribution in space in relation to the marine environment will help to understand the systems that maintain them, especially the specific oceanographic context, which is poorly known in most cases, and to model properly their population dynamics and their aggregation at fishing and prespawning grounds. The success in demonstrating a plausible relationship between North Sea herring distributional abundance and bathymetry, seabed substrate, and zooplankton suggests that the methods used here could be successfully applied to other pelagic or even demersal fish. It is more than likely that demersal species would exhibit an even stronger attachment to particular substrate types and water depth zones; hence the current methodology might prove fruitful.

Currently, there is a need for improved methods of fish stock assessment. A substantial amount of money and effort is directed annually toward fishery research surveys. Results from the present study could have a direct impact on fish stock assessment and management decisions. Convincing, stable relationships between species and environmental variables, which have also been quantitatively identified, can be used for more appropriate stratification in future acoustic surveys. This could result in more accurate species stock biomass estimates. Furthermore, each species has a spatial "signature"; characterizing this in relation to controlling environmental covariates could be advantageous. The present results clearly showed that environmental variables can be used to characterize specific ranges of fish values. These could be either the highest concentrations of fish or the lowest (i.e., zero) concentrations. Thus, areas where highest densities may occur can reasonably be predicted. Apart from enabling us to conceive further the factors that influence the habitat choice and clustering of a pelagic fish species, this could also be of great assistance in future surveys and stock assessment issues. More precisely, it can be used as a means of reducing the variance in abundance estimates by providing additional information for the part of the survey area that requires more sampling effort, due to high variability, through covariates that are easy to measure. In other words, it could be used as an indicator of areas where it is worth increasing the sample density for estimation of the global stock biomass because they are sufficiently rich and they have a high variance, a phenomenon common in pelagic schooling species. Conversely, it can be used as an indicator of areas where is worth decreasing the sampling intensity because of a consistent low abundance.

The present work has shown that the distribution of a pelagic fish species is a complex phenomenon related to a variety of environmental and biotic factors. It should be remembered that the relationships demonstrated are likely to be probabilistic. At any one time, most of the fish will be found in "optimal" areas. However, herring is a typical migratory and highly mobile pelagic species, and given the variety of interacting environmental factors, it is to be expected that, at any one time, some of the fish will be responding to different stimuli than others, resulting in a complex and variable distribution. Notwithstanding this, it has been demonstrated that there are relationships that are fairly consistent from year to year and that match previous hypotheses. Clearly, additional years of data would be useful in further testing the stability and continuity of the suggested relationships. It is likely that other factors (e.g., currents, wind velocity, temperature, salinity) are also important and should be evaluated in the future taking into account that the expected phenomenon has a given degree of probability of occurrence.

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Influence of nitrogen to phosphorus supply ratios and physicochemical conditions on cyanobacteria and phytoplankton species composition in the Experimental Lakes Area, Canada

S.N. Levine and D.W. Schindler

Abstract: To test the hypothesis that N:P supply ratios influence phytoplankton species composition, and particularly that cyanobacteria are favored by a low ratio, mesocosms at one pelagic and two littoral sites within the Experimental Lakes Area, Ontario, were fertilized for 10–12 weeks with similar amounts of P but different amounts of N. Total N:P supply (L_N:L_P) ratios (fertilizer plus natural inputs) ranged from 8:1 to 50:1. Nitrogen deficiency was detected in all mesocosms with L_N:L_P ratios <17:1, but N_2-fixing *Anabaena* gained dominance only in the low-N:P pelagic mesocosms, and only in late summer. Cryptophytes and (or) chlorophytes dominated littoral mesocosms at all N:P ratios, while *Pseudoanabaena catenata*, a nonheterocystous cyanobacterium, was the late-summer dominant in pelagic mesocosms with L_N:L_P ratios >17:1. Canonical correlation analysis related cyanobacterial dominance to high P and low CO_2 availability. Low light intensities and low N:P ratios also favored heterocystous (but not nonheterocystous) cyanobacteria. Total phytoplankton biomass and productivity increased with L_N:L_P ratio, while periphyton growth was maximal at low N:P ratios. Nitrogen limitation of phytoplankton may encourage blooms of N_2 fixers or drive productivity down to the sediment surface where N is more available.

Résumé : Pour vérifier l'hypothèse que les ratios N:P dans les apports influent sur la composition par espèces du phytoplancton, et particulièrement que les cyanobactéries sont favorisées par un faible ratio, on a fertilisé durant 10–12 semaines avec des quantités similaires de P et des quantités différentes de N des mésocosmes à un site pélagique et à deux sites littoraux de la Région des lacs expérimentaux, en Ontario. Les ratios N:P des apports totaux de ces éléments (L_N:L_P) (fertilisant plus apports naturels) variaient de 8:1 à 50:1. Le manque de N a été détecté dans tous les mésocosmes dont les ratios L_N:L_P étaient inférieurs à 17:1, mais les *Anabaena* fixatrices de N_2 ne sont devenues dominantes que dans les mésocosmes pélagiques à faible ratio N:P, et seulement à la fin de l'été. Les cryptophytes et (ou) les chlorophytes ont dominé les mésocosmes littoraux à tous les ratios N:P, tandis que *Pseudoanabaena catenata*, une cyanobactérie sans hétérocyste, a été l'espèce dominante à la fin de l'été dans les mésocosmes pélagiques dont les ratios L_N:L_P étaient supérieurs à 17:1. L'analyse de corrélation canonique a relié la dominance des cyanobactéries à une disponibilité de P élevée et de CO_2 faible. Les faibles intensités lumineuses et les ratios N:P bas ont aussi favorisé les cyanobactéries à hétérocystes (mais pas les cyanobactéries sans hétérocyste). La biomasse et la productivité totales du phytoplancton augmentaient en raison directe du ratio L_N:L_P, tandis que la croissance du périphyton était maximale quand les ratios N:P étaient bas. La limitation de la croissance du phytoplancton due à un manque de N peut encourager la prolifération des fixateurs de N_2 ou déplacer la productivité à la surface des sédiments, où le N est plus disponible.

[Traduit par la Rédaction]

Introduction

The relative availability of resources in the aquatic environment may play a major role in structuring phytoplankton communities (Tilman et al. 1982; Harris 1986; Sommer et al. 1986). Of particular importance may be N:P supply (L_N:L_P) ratios. In most lakes, P, N, or both nutrients limit phytoplankton growth (Hecky and Kilham 1988). Thus, interspecific differences in compositional N:P ratios, in the dynamics of inorganic N and P uptake, and in the extent to which dissolved organic or atmospheric sources of nutrient are exploited may determine which species can coexist at specific L_N:L_P ratios (Rhee and Gotham 1980; Tilman et al. 1982; Harris 1986; Kilham et al. 1996). While the impact of L_N:L_P ratios on competitions between eucaryotic algal species has received little attention to date, the hypothesis that cyanobacteria are favored by low L_N:L_P ratios has fostered

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considerable research. Its basis is principally the ability of heterocystous cyanobacteria to fix atmospheric N_2 and thus gain access to a vast N source during periods of dissolved inorganic N (DIN) scarcity (Schindler 1977). No eucaryotic alga is capable of N_2 fixation, while nonheterocystous cyanobacteria are either restricted to fixation under anaerobic conditions or cannot fix at all. Because N_2 fixation is a light-dependent process (Lewis and Levine 1984), and there is generally little light in anaerobic hypolimnia or sediments, heterocystous cyanobacteria are the principal N_2 fixers in lakes. Some versions of the low-N:P hypothesis (e.g., Smith 1983, 1985) contend that nonheterocystous as well as heterocystous cyanobacteria are favored by low L_N:L_P ratios. However, there is little theoretical basis for this supposition. All cyanobacteria store surplus N in cyanophytin and thus may be able to weather short episodes of N deficiency better than eucaryotes, but long-term adaptations to N scarcity, such as unusually efficient exploitation of inorganic or organic N, or particularly low N:P compositional ratios, have not been substantiated for cyanobacteria in general (Reynolds 1984; Harris 1986). Because most of the algae that form offensive surface scums are heterocystous cyanobacteria (*Microcystis* is a notable exception), the low-N:P hypothesis is of great interest to lake managers; it suggests that blooms might be controlled through N additions to lakes as well as through reductions in P supply.

Evidence for an impact of N:P ratios on phytoplankton community structure includes experiments in continuous cultures in which cyanobacteria have outcompeted other algae at low but not high N:P ratios (e.g., Tilman et al. 1982, 1986), natural phytoplankton successions in lakes undergoing eutrophication or recovery from eutrophication that have tracked changes in N:P ratios (e.g., Tilman 1982; Sommer et al. 1986), and empirical analyses in which it has been shown that cyanobacteria are minor components of the phytoplankton at very high total N to total P (TN:TP) ratios (>64:1; Smith 1983) and that N_2 fixation is substantial only when N:P supply ratios are <22:1 (Flett et al. 1980). Especially convincing have been experiments conducted within the Experimental Lakes Area (ELA) of northwestern Ontario, in which lakes fertilized with N and P at an N:P ratio of 11:1 developed blooms of heterocystous cyanobacteria, while those fertilized at ratios of 29:1 to 31:1 did not (Schindler 1977). When the N:P supply ratio to Lake 227 was reduced from 29:1 to 11:1, heterocystous *Anabaena* gained dominance for the first time in 5 years of fertilization.

In this paper, the role that N:P supply ratios play in structuring phytoplankton communities is explored in large (10-m-diameter) mesocosms at three sites (two littoral and one pelagic) within the ELA. Mesocosms were fertilized for 10–12 weeks with similar amounts of P, but at two very different N:P ratios, one (33:1) great enough to induce general P limitation and the other (4.4:1) so low that N limitation was expected among all non-N_2-fixing phytoplankton. Phytoplankton composition, biomass, and productivity were tracked and treatment effects identified with repeated measures analysis of variance (ANOVA). Mesocosms were used to provide the "replication", untreated controls, and nearly uniform background conditions that whole-lake experiments lack. Because phytoplankton successions may be influenced by factors other than N:P ratios, we included in our study the monitoring of a suite of physicochemical factors believed to be important in species selection and used correlation analysis (Pearson product-moment and canonical) to identify relationships. Finally, periphyton biomass and productivity in the mesocosms were measured to determine whether this community was sufficiently well developed to divert resources away from phytoplankton, diminishing their growth and affecting the dynamics of interspecific competition.

Materials and methods

Lake descriptions

Our experiments took place in ELA Lakes 303 and 302S (previously described in Levine and Schindler 1989, 1992). Both lakes are low in alkalinity (<100 μequiv.$\cdot L^{-1}$) and conductivity (10–15 $\mu S \cdot cm^{-1}$) and naturally oligotrophic (Armstrong and Schindler 1971; Schindler et al. 1980). Lake 303, with a mean depth of 1.5 m, mixes continually during the ice-free season (May–October), while Lake 302S (mean depth 5.1 m) stratifies (epilimnion depth 2–4 m). Both lakes have sediments that are flocculent (>90% water) and highly organic (loss on ignition about 30% of dry weight), except near inflows, where sands may be present (Brunskill et al. 1971). Phosphorus flux from sediments is minimal even under anoxia, but N recycling can be substantial (Schindler et al. 1987; Levine and Schindler 1992). Chrysophytes and diatoms are major components of the phytoplankton year-round (Kling and Holmgren 1972; Findlay 1981), while copepods (e.g., *Diaptomus minutus*, *Acanthocyclops vernalis*, *Mesocyclops edax*, *Epischura lacustris*, *Tropocyclops prasinus mexicanus*) and rotifers dominate the zooplankton (Malley et al. 1988). Cladocera (*Holopedium gibberum*, *Diaphanosoma birgei*, *Bosmina longirostris*, and *Daphnia retrocurva*) are occasionally abundant.

Lake 302S had no history of manipulation at the time of our experiment, whereas Lake 303 had been fertilized with N and P (N:P = 31:1) during the two previous summers. The phytoplankton community of the fertilized lake was dominated by desmids, cryptophytes, and, at times, filamentous nonheterocystous cyanobacteria (*Lyngbya*, *Oscillatoria*, and *Pseudoanabaena*; Levine and Schindler 1989). By the initiation of our experiments (10 months after fertilization ended), chrysophytes had regained dominance and algal standing crops and P chemistry were back to prefertilization levels. Nitrogen outflux from sediments, however, was still well above historical levels (Levine and Schindler 1989).

Mesocosm design and treatment

Mesocosms were installed in Lake 303 at a depth of 2 m, above sandy sediments in littoral Lake 302S (also 2 m depth), and in the deepest portion of Lake 302S (7–9 m depth). At the Lake 302S sites, duplicate open-bottomed mesocosms were fertilized at N:P ratios of 33:1 and 4.4:1. In Lake 303, two open-bottomed mesocosms and one floored mesocosm were fertilized at each N:P ratio, while one unfloored mesocosm and one floored mesocosm were included as unfertilized controls. Two weeks into the experiment, the floored N:P = 33 mesocosm was torn apart by sediment gases, and thus abandoned.

The mesocosms used in the experiments have been described previously (Levine and Schindler 1989, 1992). All were 10-m-diameter cylinders of clear polyethylene suspended from frames at the lake surface and weighted at the bottom. The walls of the littoral mesocosms extended several centimetres into the sediments, while those of the pelagic mesocosms terminated below the thermocline at a depth of 6 m. Plastic floors were attached to walls with strips of Polyzip and were equipped with venting systems to divert sediment gases to the atmosphere.

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Table 1. Mean values of various physicochemical and biological parameters for the mesocosms of Lake 303 during the period of fertilization.

		Mesocosm						
		Unfertilized		N:P = 4			N:P = 33	
Parameter	Lake	Control	Bottomed	A	B	Bottomed	A	B
L_N:L_P	—	1711	92	21	24	13	50	49
τ, days	401	71	235	470	307	325	314	198
TP, μM	0.31	0.33	0.32	1.12	1.11	1.29	1.06	0.85
TDP, μM	0.15	0.14	0.12	0.34	0.34	0.69	0.38	0.22
TN, μM	84	75	43	53	68	42	105	91
DIN, μM	47	36	1	1	18	1	48	41
TN:TP	276	244	137	49	64	38	101	106
DIN:TP	158	122	3.6	0.8	16	1.1	43	47
DOC, μM	582	623	690	718	637	680	637	625
DIC, μM	169	161	118	149	160	126	191	163
CO_2, μM	44	39	26	30	35	24	41	34
pH	6.75	6.82	6.85	6.91	6.85	6.95	6.81	6.90
ε, metres	0.8	0.9	0.6	1.0	1.0	0.7	1.2	1.2
Light, einsteins·m^{-2}·day^{-1}	8.1	6.6	7.8	6.1	6.4	7.5	5.9	5.8
z_p:z_m	3.9	2.5	3.4	2.2	2.3	3.2	2.1	2.0
C fixation, mmol·m^{-2}·day^{-1}	7	7	6	25	26	10	32	45
Chlorophyll *a*, μg·L^{-1}	3	4	5	13	11	6	17	24
Phytobiomass, mg·L^{-1}	0.74	0.64	0.55	2.36	1.68	0.66	2.87	3.55
Periphyton, g	—	68	—	129	381	—	66	62
Periphyton, as % total algae	—	18	—	8	20	—	2	18

Note: L_N and L_P, total N and P inputs (natural and fertilizer); τ, water residence time; ε, light extinction coefficient; z_p, depth of the photic zone; z_m, depth of the mixed layer. Light is averaged over the mixed layer. Values for individual dates can be found in Levine (1983) and Levine and Schindler (1992).

The mesocosms were fertilized weekly with phosphoric acid and sodium nitrate. In Lake 303, the P dose was 0.32 μmol·L^{-1}·$week^{-1}$ and the N dose either 11 or 1.4 μmol·L^{-1}·$week^{-1}$. The pelagic mesocosms of Lake 302S initially received the same N and P doses as the Lake 303 mesocosms. However, because of thermally induced increases in epilimnion depth, volumetric loading of nutrients to these mesocosms decreased over time. At the end of the experiment, our weekly P additions (which did not change over time) yielded a concentration of 0.23 μmol P·L^{-1}. For the littoral mesocosms of this lake, P addition rates were varied (0.39–0.52 μmol P·L^{-1}) in an attempt to standardize L_pV_o (where L_p is microlitres of P per litre per week and V_o is litres of water exchanged weekly through leakage) and thus account for differences between mesocosms in their water exchange rates (as determined by tritium additions; see Levine and Schindler 1992). This procedure was not entirely successful, as P tended to accumulate more in the mesocosms that received more P (Tables 1 and 2). Enough N was added to achieve the desired N:P supply ratios. For the Lake 303 mesocosms, fertilization began on 10 August 1977 and continued until 25 October 1977, when ice formed on the lake. The experiments in the Lake 302S mesocosms were begun earlier in the year, on 10 June 1978, and ended on 5 September, when the thermocline of the lake deepened below 6 m and the mesocosms were flushed with outside water. The mesocosms exchanged little water with the surrounding lakes. Water residence times (τ) ranged from 28 to 112 days in Lake 302S and from 198 to 470 days in Lake 303 (Tables 1 and 2).

Sample collection and analysis

Solar insolation was measured continuously during the experiment at a nearby meteorological station with an Eppley pyranometer and calibration factors used to estimate photosynthetically available radiation. Light attenuation with depth was assessed biweekly in each mesocosm using a LiCor cosine-corrected submersible quantum probe. Average light intensity (I_{ave}) within the mixed layer was calculated from average daily insolation (I_0), the rate of light extinction, and depth of the mixed layer (z_m) using the equation

$$(1) \qquad I_{ave} = I_0 \cdot \int_0^{z_m} (f_z \mathrm{d}z)$$

where f_z is the fraction of surface light penetrating to depth z. Vertical profiles for water temperature were determined biweekly with a YSI thermister at the central sampling station of each lake and on two or three occasions in the mesocosms themselves. Temperature profiles were similar inside and outside the mesocosms (Levine 1983).

Depth-integrated water samples were collected from the mesocosms and the mixed layer of the lakes biweekly with a PVC pipe (length 2 m for littoral and 3 m for pelagic mesocosms) and a rubber stopper. Three or four sites within each mesocosm were sampled and the water pooled. Among the chemical and biochemical fractions measured (using the procedures of Stainton et al. 1977)

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Table 2. Mean values of various physicochemical and biological parameters for the mesocosms of Lake 302S during fertilization.

		Littoral mesocosms				Pelagic mesocosms			
		N:P = 4		N:P = 33		N:P = 4		N:P = 33	
Parameter	Lake	A	B	A	B	A	B	A	B
L_N:L_P	—	14	17	33	33	12	8	34	36
τ, days	—	43	112	36	44	30	44	28	28
TP, μM	0.26	1.24	1.23	1.69	1.11	1.18	1.11	1.14	1.02
TDP, μM	0.12	0.82	0.82	0.53	0.45	0.37	0.41	0.39	0.32
TN, μM	26	28	28	72	60	36	33	58	57
DIN, μM	1	1	1	12	19	2	2	20	19
TN:TP	101	23	24	44	55	32	32	52	56
DIN:TP	5.8	1.4	1.8	17	18	1.7	2.4	18	19
DOC, μM	412	392	396	465	487	380	389	434	433
DIC, μM	64	56	62	52	56	54	53	60	54
CO_2, μM	13	8	9	4	4	8	6	6	6
pH	6.9	7.2	7.2	8.4	8.3	7.4	7.4	7.9	8.0
ε, metres	0.5	0.5	0.5	1.2	0.8	0.6	0.6	0.7	0.7
Light, einsteins·m^{-2}·day^{-1}	17	21	22	16	18	16	17	14	14
z_p:z_m	2.7	4.5	5.1	2.6	3.1	2.5	2.5	2.0	2.0
C fixation, mmol·m^{-2}·day^{-1}	19	11	10	126	63	58	41	104	154
Chlorophyll *a*, μg·L^{-1}	4	6	4	79	18	14	11	19	17
Phytobiomass, mg·L^{-1}	0.67	0.61	1.49	7.46	3.93	1.44	1.43	2.05	2.09
Periphyton, g	—	243	396	108	394*	73	88	31	31
Periphyton, as % total algae	—	95	81	6	20	9	20	8	7

Note: L_N and L_P, total N and P inputs (natural and fertilizer); τ, water residence time; ε, light extinction coefficient; z_p, depth of the photic zone; z_m, depth of the mixed layer. Light is averaged over the mixed layer. Values for individual dates can be found in Levine (1983) and Levine and Schindler (1992).

*Substantially more periphyton was present on the sampled periphyton strip than on the walls. Thus, this value is unrealistically high.

were chlorophyll *a*, pH, particulate P, N, and C, total dissolved N and P (TDN and TDP), NO_3-N, NH_4-N, dissolved inorganic carbon (DIC), and dissolved organic carbon (DOC). CO_2 concentrations were calculated from pH, DIC, and temperature (Garrels and Christ 1961). Phytoplankton were preserved in Lugol's solution and counted with an inverted microscope. Counting continued to 100 cells of the most abundant species or to 100 fields (minimum of 10 fields). Phytobiomass was calculated from cell dimensions and geometric shape assuming a specific gravity of 1.0 (Wetzel and Likens 1991).

Primary productivity was estimated biweekly using the incubator technique and numerical model of Fee et al. (1992). To normalize across sampling dates, we assumed cloudless conditions. When heterocystous cyanobacteria were present, we used the same incubator and model and the acetylene reduction method to estimate N_2 fixation (Levine and Schindler 1992). Periphyton growth on the mesocosm walls was quantified by hanging strips of wall material at the center of each mesocosm at the beginning of the study and removing them after 5 weeks in Lake 303 and after 3 and 8 weeks in Lake 302S. Algae were scrapped from the strips and suspended in filtered lake water, which was then treated like a phytoplankton sample. The total biomass of periphyton on mesocosm walls was estimated from the average biomass per unit area on the strips and wall area. Periphyton growth within and on sediments was generally ignored. However, two of the littoral mesocosms in Lake 302S (those fertilized at an N:P ratio of 4.4:1) developed benthic mats of filamentous periphyton several centimetres thick that had to be accounted for. For these mesocosms, we included the area of the sediment in our estimate of periphyton biomass. This approach probably substantially underestimated the actual amount of benthic periphyton, as algal densities were visibly lower on the strips than on sediments.

Data analyses

Nitrogen and P mass balances were constructed for each of the mesocosms from the data on biweekly changes in nutrient concentration, water exchange rates (obtained from the rates of loss of added tritium), rainfall volumes and chemistry, and N_2 fixation. The details of these calculations and the complete results are presented in Levine and Schindler (1992). Only final values obtained for L_N:L_P ratios are reported here.

To test the statistical significance ($P = 0.05$) of the effect of N:P fertilization on the biology and water chemistry in the mesocosms of each lake, we used two-factor repeated measures ANOVA (Winer 1971) with time as the repeated measure. Because ANOVA cannot use data from unreplicated treatments (which have no degrees of freedom), the significance of differences between unreplicated treatments (the N:P = 4 floored mesocosm, the unfertilized control mesocosms, and the epilimnions of the two lakes) and replicated treatments was tested with *t* tests. In these tests, we estimated population variance from the between-subjects mean squares

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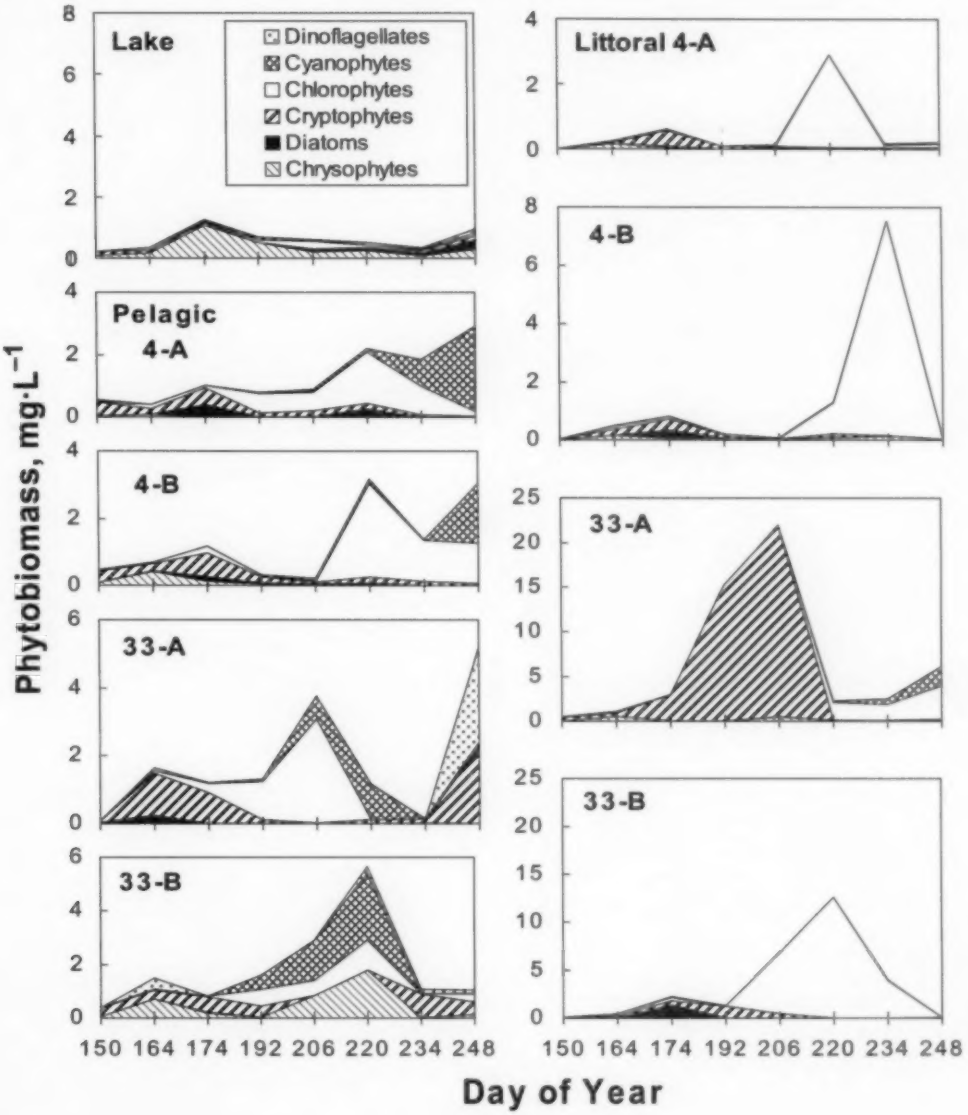
Fig. 1. Phytoplankton species composition and biomass in Lake 302S and its mesocosms during the fertilization experiments that began on 10 June (day 161). Numbers refer to the N:P ratio of the fertilizer and letters to treatment duplicates A and B (unfloored mesocosms).



of the repeated measures ANOVA (using log-transformed data). Correlations between variables were sought with Pearson product-moment and canonical correlation analysis (Darlington 1975; Varis 1991). Data that were not normally distributed were either log transformed (physicochemical parameters and phytoplankton group biomasses) or transformed to the arcsine (group percentages) prior to the analysis. Canonical correlation analysis relates one set of potentially interrelated variables (such as phytoplankton composition) to another set of variables (such as physicochemical parameters) in a way that maximizes the correlation. The residuals of the first relationship are then analyzed to uncover additional associations. Further details, along with examples of the method's application to phytoplankton studies, are available in Varis (1991).

Results

Unfertilized lakes and mesocosms

Chrysophytes dominated the phytoplankton of Lake 302S and chrysophytes and small chlorophytes (first *Monoraphidium minutum* and then *Pediastrum tetras*) the phytoplankton of Lake 303 during the experiments in mesocosms (Figs. 1 and 2). Phytoplankton communities in the unfertilized mesocosms of Lake 303 were similar to those in the lake, except that *Pediastrum tetras* was lacking in the mesocosm with a plastic floor, possibly because recruitment of benthic resting stages was blocked. Levels of phytobiomass,

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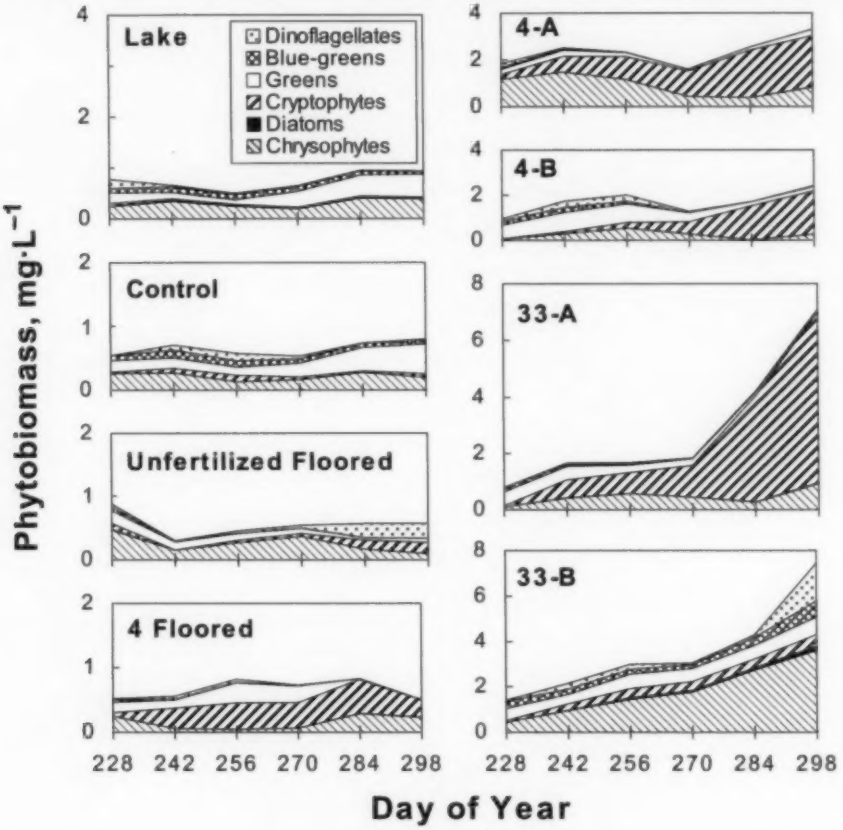
Fig. 2. Phytoplankton species composition and biomass in Lake 303 and its mesocosms during the fertilization experiments that began on 10 August (day 222). Numbers refer to the N:P ratio of the fertilizer and letters to treatment duplicates A and B.



chlorophyll *a*, and primary productivity in the unfertilized mesocosms and lake were insignificantly different at P = 0.5. The only significant difference in water chemistry observed between the open-bottomed control mesocosm and the lake was greater nitrate concentrations in the latter, probably because it received watershed inputs shut out by mesocosm walls (Levine and Schindler 1992).

Phytoplankton response to fertilization

Fertilization of mesocosms with P at 35–40 times the natural allochthonous supply level and with enough N to yield an N:P supply ratio of 33:1 increased the mean primary productivity, phytobiomass, and chlorophyll *a* concentrations in mesocosms by four- to nine-fold (but in one littoral mesocosm of Lake 302S, chlorophyll *a* increased by 22 times; Tables 1 and 2). Response to fertilization with the same amount of P, but less N (N:P = 4.4:1), was much less dramatic. In the littoral mesocosms of Lake 302S and in the floored mesocosm of Lake 303, primary productivity and biomass increased by no more than two times and often were at lake levels (the means were insignificantly different from those of the lakes at P = 0.05). Productivity and biomass levels were similarly low in the pelagic mesocosms for several weeks of fertilization but, on the appearance of N_2-fixing cyanobacteria, rose to levels similar to those in neighboring N:P = 33 mesocosms (Figs. 2–4). Repeated measures ANOVA indicated no N:P ratio effect on phytobiomass and primary productivity for the pelagic experiment but did suggest a significant effect on chlorophyll *a* concentration. In the N:P = 4 unfloored mesocosms of Lake 303, fertilization increased biomass and productivity by three times (significantly different from the control and lake at P = 0.05). The levels attained were half those in the N:P = 33:1 mesocosms, however.

Mesocosm fertilization altered phytoplankton species composition, even in those mesocosms that maintained low levels of algal biomass and productivity (Figs. 1 and 2). The initial successions were similar for both N:P supply ratios, suggesting that increased P supply was the principal factor forcing species change. Chrysophytes and, in Lake 303, *Monoraphidium minutum* and *Radiocystis geminata* increased in abundance. Within 6 weeks, however, these species were replaced by cryptophytes in all but one fertilized mesocosm (an N:P = 33 mesocosm in Lake 303). *Rhodomonas minuta* formed near monocultures (accounting for 50–90% of total biomass) in the Lake 303 mesocosms, while the dominants in Lake 302S were *Cryptomonas rostratiformas* and *Cryptomonas marsonii*. The mesocosm that escaped cryptophyte dominance remained chrysophyte dominated throughout the study (especially important were *Chrysochromulina brevi-*

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Fig. 3. Chlorophyll *a* concentrations in lakes and mesocosms during the fertilization experiments that began on 10 August (day 222) in Lake 303 and on 10 June (day 161) in Lake 302S. ◇◆, N:P = 4 unfloored; +, N:P = 4 floored ; ○●, N:P = 33 unfloored; ×, lake; □ control; ▲, unfertilized floored.

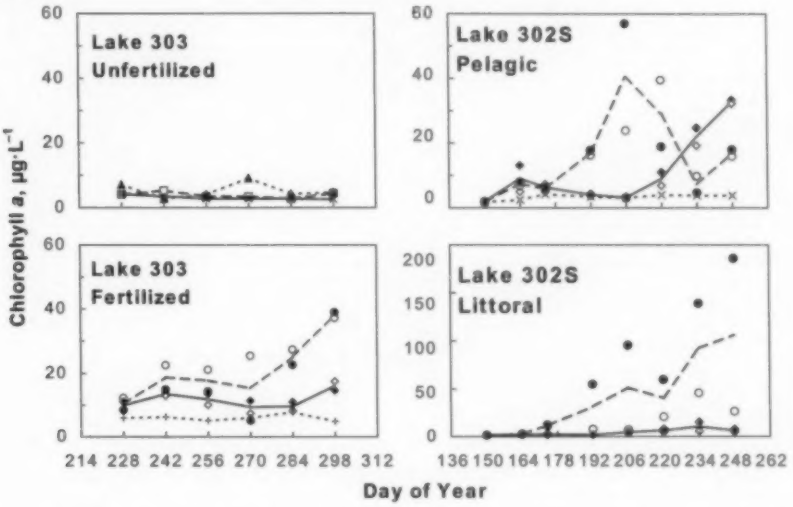
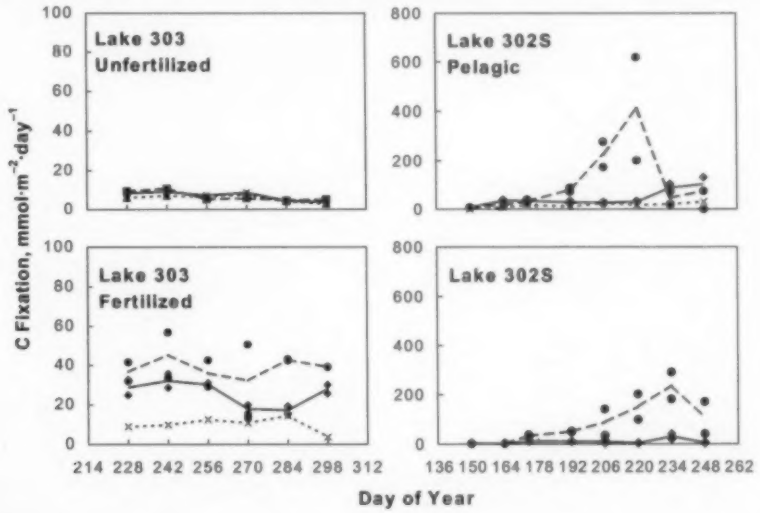


Fig. 4. Carbon fixation rates in lakes and mesocosms during the fertilization experiments. Rates were estimated for cloudless skies, rather than actual solar conditions. Fertilization of mesocosms began on 10 August (day 222) in Lake 303 and on 10 June (day 161) in Lake 302S. ◇◆, N:P = 4 unfloored; +, N:P = 4 floored; ○●, N:P = 33 unfloored; ×, lake; □, control; ▲, unfertilized. floored.



turra, *Mallomonas pseudocoronata*, *Mallomonas longiseta*, and *Ochromonas stellaris*). The physicochemical environments of the two N:P = 33 mesocosms in Lake 303 were similar (Table 1), suggesting that an unmeasured variable (perhaps grazer density or type) caused the divergent successions.

Cryptophytes maintained dominance in the Lake 303 mesocosms (at both N:P ratios) until the experiment's end. In Lake 302S, the cryptophyte phase lasted 3–8 weeks and in seven of eight mesocosms involved little biomass relative to the blooms of chlorophytes and cyanobacteria that followed. However, one littoral N:P = 33 mesocosm (the one with exceptionally high chlorophyll *a* concentrations) supported a major "bloom" of *Cryptomonas rostratiformas* (biomass reached 22 mg·L^{-1}), which depleted dissolved nutrients and allowed for only small development of chlorophyte and cyanobacterial populations later in the season (Fig. 2).

Chlorophytes rose to dominance or subdominance in the Lake 302S mesocosms in late June to mid-July. The species that prevailed depended on the N:P ratio of the fertilizer applied. In the N:P = 33 mesocosms (littoral and pelagic), *Characiochloris incrassata* accounted for the most biomass, while *Schoederia setigeria* dominated in the littoral and *Dictyosphaerium pulchellum* in the pelagic N:P = 4 mesocosms. *Monoraphidium* (several species) was abundant in most mesocosms. Five of the eight Lake 302S mesocosms

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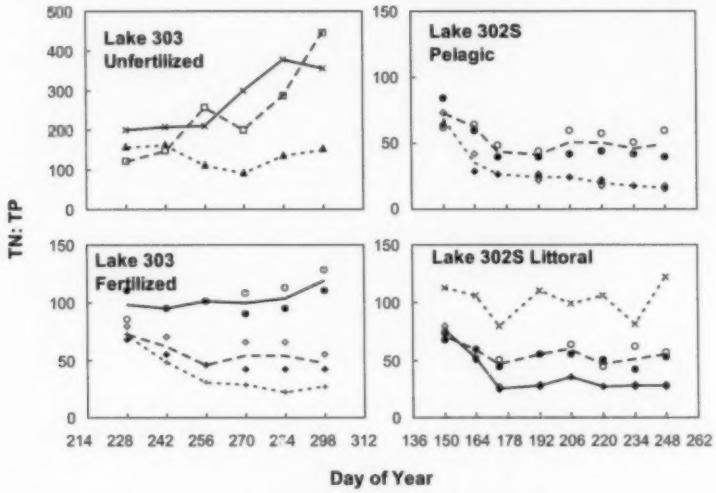
Fig. 5. TN:TP in lakes and mesocosms during the fertilization experiments that began on 10 August (day 222) in Lake 303 and on 10 June (day 161) in Lake 302S. ◇◆, N:P = 4 unfloored; +, N:P = 4 floored; ○●, N:P = 33 unfloored; ×, lake; □, control; ▲, unfertilized floored.



attained maximum phytobiomass during chlorophyte dominance (the exceptions being the littoral N:P = 33 mesocosm with the *Cryptomonas* bloom and the pelagic N:P = 4 mesocosms).

Chlorophytes dominated until the experiment's end in the littoral zone of Lake 302S, whereas in the pelagic zone, a further succession, this time to cyanobacteria, occurred. *Pseudoanabaena catenata* gained dominance in the duplicate N:P = 33 mesocosms, while *Anabaena circinalis* grew to bloom proportions in the N:P = 4 mesocosms (*Anabaena planctonica* was subdominant). *Anabaena* fixed N_2 at rates of up to 42 mg $N \cdot m^{-2} \cdot day^{-1}$ (Levine and Schindler 1992) and brought phytoplankton biomass up to levels similar to those in the N:P = 33 mesocosms (Fig. 1). Algal biomass was still increasing in these mesocosms when lake overturn occurred and the mesocosms were flushed, ending the experiment.

As the thermocline deepened in late September and nutrient-rich metalimnetic waters were mixed into the epilimnion, yet one more succession took place in the pelagic N:P = 33 mesocosms: cyanobacteria were replaced by the same species of *Cryptomonas* that had been common in early summer. Dinoflagellates also appeared in appreciable numbers, although the high biomass depicted in Fig. 2 represents the presence of only a few large cells and thus may not be accurate.

Repeated measures ANOVA indicated a strong time effect on the biomass and relative biomass of the various phytoplankton divisions in mesocosms, but very little impact of N:P ratio. The biomass of the most abundant division of each experiment (cryptophytes in Lake 303 and chlorophytes in Lake 302S) was shown to be significantly greater in the N:P = 33 than in the N:P = 4 mesocosms, due to lower incidence of N limitation, but no impact on the relative abundance of the various divisions was apparent. We reanalyzed our data, segregating cyanobacteria into heterocystous and nonheterocystous members, and found that the the former were more abundant and more dominant at an N:P = 4 fertilization ratio, while the latter attained greater biomass and dominance at an N:P fertilization ratio of 33:1 ($P = 0.5$).

physicochemical conditions in the mesocosms

ANOVA assumes that treatments are well defined and background conditions not treatment dependent. This is often not the case in mesocosm experiments, hence the common reference to mesocosms as "pseudoreplicates". Physicochemical conditions in the mesocosms were examined to determine whether the expected dichotomy of N- and P-limiting habitats was achieved, whether the background environment was similar among mesocosms, and whether conditions varied greatly temporally. Mesocosm nutrient inputs and outputs also were monitored to estimate total N:P supply (L_N:L_P) ratios.

We found that L_N:L_P ratios often diverged substantially from the fertilization ratios, principally because substantial amounts of N were recycled from sediments (Tables 1 and 2) (for details, see Levine and Schindler 1992). Mean L_N:L_P ratios in the N:P = 4 mesocosms ranged from 8:1 to 24:1, while those in the N:P = 33 mesocosms ranged between 31:1 and 50:1. TN:TP ratios in the mesocosms were highly correlated with L_N:L_P ratios, but were greater in magnitude, probably because TN generally contains more refractory material than TP (White et al. 1985). TN:TP ratios are generally high in unfertilized ELA lakes (>100:1). Thus, fertilization at both N:P ratios caused TN:TP ratios to fall during the first 6 weeks of fertilization. Thereafter, the values were relatively stable (Fig. 5). The means for the N:P = 4 and N:P = 33 mesocosms in Lake 302S ranged from 23:1 to 32:1 and from 44:1 to 56:1, respectively, while in Lake 303, the same treatments produced TN:TP ratios of 38:1 to 64:1 and 101:1 to 106:1, respectively. DIN:TP ratios were very low (1:1 to 2:1) in six of seven N:P = 4 mesocosms; in the seventh (a Lake 303 mesocosm), the average was 16:1. DIN:TP ratios ranged from 9:1 to 43:1 in the N:P = 33 mesocosms. The variability of L_N:L_P, TN:TP, and DIN:TP ratios among meso-

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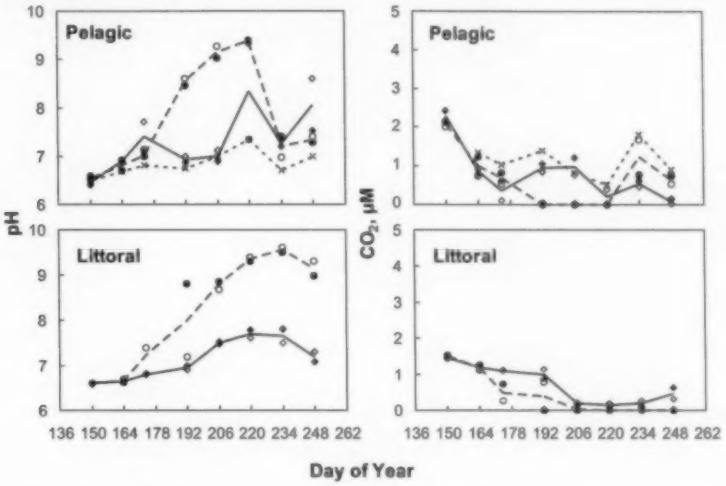
Fig. 6. pH and CO_2 concentrations in Lake 302S and its mesocosms during the fertilization experiments that began on 10 June (day 161). ◇◆, N:P = 4; ○●, N:P = 33; ×, lake.



cosms of the same fertilization scheme argues against strong reliance on repeated measures ANOVA in interpreting experimental results and for supplementary correlation analysis.

TP concentrations in the fertilized mesocosms rose steadily throughout the experiments, reaching levels typical of eutrophic lakes (the experimental means were 1.0–1.8 versus 0.2–0.3 µM in the oligotrophic lakes). In 10 mesocosms, the accumulating P was mostly particulate (i.e., in algae, bacteria, and detritus), but in three mesocosms, it was principally dissolved, suggesting incomplete biological use of the P fertilizer (Tables 1 and 2) (Levine and Schindler 1992). These mesocosms were the plastic-floored mesocosm of Lake 303 and the littoral mesocosms of Lake 302S.

TN concentrations also increased during the first 8–10 weeks of fertilization and then leveled off in mesocosms without N_2 fixation. Where N_2 fixation occurred, TN concentrations increased by about 60% (Levine and Schindler 1992). Large N fluxes from sediments had a major impact on N concentrations in Lake 303. The lake had mean TN and DIN concentrations of 84 and 47 µM, respectively, and the N:P = 33 mesocosms means of 91–105 and 41–48 µM, respectively. That DIN concentrations were not elevated by nitrate additions to these mesocosms suggests that most of the nitrate was either taken up by organisms or denitrified. Fertilization at an N:P ratio of 4.4:1 resulted in TN and DIN concentrations below those in the unfertilized lake (TN = 53–68 µM in the unfloored and 42 µM in the floored mesocosms; DIN = 1 and 18 µM in the unfloored and 1 µM in the floored mesocosms), most likely because the added P increased phytoplankton N use. In Lake 302S, background TN and DIN concentrations were 26 and 1 µM, respectively. Fertilization at an N:P ratio of 33:1 yielded mean TN and DIN concentrations of 58 and 28 µM, respectively, while fertilization at an N:P ratio of 4.4:1 resulted in concentrations near background levels, 28–36 and 1–2 µM, respectively.

The pH and the CO_2 concentration were monitored because they are variables believed to influence phytoplankton species composition, especially cyanobacterial success (Shapiro 1990). The mesocosms in Lake 303 remained near neutral in pH throughout the experiment and maintained fairly high CO_2 concentrations (0.8–4.5 µM), perhaps because their organic sediments provided alkalinity (Schiff and Anderson 1987). By contrast, in Lake 302S, only the very unproductive N:P = 4 mesocosms of the littoral zone maintained neutrality and had moderate levels of CO_2 throughout the experiment (Fig. 6). In the N:P = 4 mesocosms of pelagic Lake 302S, pH rose above 8.0 and CO_2 concentrations fell below 0.2 µM, the critical level below which C fixation is generally C limited (Lund 1970), during the last month of fertilization. In all of the N:P = 33 mesocosms of Lake 302S, pH remained above 8.0 for at least half of the study and >9.0 for 2–4 weeks. For more than half of the experiment, CO_2 concentrations were <0.2 µM.

Major changes in temperature, solar radiation, and mixed layer depth occurred over the several-week-long experiments (Levine 1983). In general, more light was available in Lake 302S than in Lake 303 (experimental means for the mixed layer 14–22 versus 6–8 einsteins·m^{-2}·day^{-1}) and temperatures were warmer (ranges 14–22 versus 5–20°C). Mixed layer depth was always to the bottom in littoral mesocosms (2 m) but varied from 3 m (May) to 5 m (early September) in the pelagic mesocosms. During both experiments, the N:P = 4 mesocosms had greater average light intensities than the N:P = 33 mesocosms because of their lower phytobiomass. The ratio of photic zone depth (z_p) to mixed layer depth (z_m) in the mesocosms was consistently >1.0 (Tables 1 and 2), suggesting that photosynthesis was not light limited (Fee et al. 1992). Dissolved O_2 concentrations were not measured in the mesocosms. However, concentrations in the mixed layers of the two lakes (which extended to the bottom of the littoral mesocosms) never dropped below 8.2 mg·L^{-1} in Lake 302S or below 6.8 mg·L^{-1} in Lake 303.

Correlation analysis

Pearson product-moment tests on the entire data set (both lakes, all dates) showed positive relationships between sev-

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Table 3. Canonical correlation analysis of environmental factors affecting the biomass and relative biomass of the major phytoplankton groups.

X variable	CV 1	CV 2	*Y* variable	CV 1	CV 2
For group biomass					
TP	0.055	0.4234	Heterocystous cyanobacteria	–0.0216	–0.0757
TN:TP	0.538	0.7788	Nonheterocystous cyanobacteria	0.6506	0.7402
pH	0.7331	–0.3096	Chlorophytes	0.1591	0.1205
Light	–0.0542	–0.2005	Chrysophytes	–0.5556	0.4923
Temperature	0.4088	0.2797	Cryptophytes	–0.4922	0.4353
For relative biomass (% of total)					
TP	–0.1118	–0.8614	Heterocystous cyanobacteria	–0.0393	–0.1975
TN:TP	0.2418	–0.1014	Nonheterocystous cyanobacteria	0.4249	–0.2009
pH	0.9593	0.3898	Chlorophytes	–0.0395	–0.4049
Light	0.0924	0.0046	Chrysophytes	–0.705	0.1987
Temperature	0.0145	–0.3094	Cryptophytes	–0.5651	–0.8469
For cyanobacterial biomass only					
TP	–0.3157	–0.2447	Heterocystous cyanobacteria	–0.0602	0.9957
TN:TP	–0.7888	–0.5501	Nonheterocystous cyanobacteria	–0.9982	0.0926
pH	–0.1182	0.5234			
Light	0.2243	–0.5117			
Temperature	–0.4624	0.3188			

Note: Both canonical variates (CV 1 and CV 2) were significant, but CV 1 accounted for more variability. The values given indicate the relative contributions of the *X* and *Y* variables to each CV. Compare CV 1 *X* variables with CV 1 *Y* variables and CV 2 *X* variables with CV 2 *Y* variables.

eral measures of both P and N availability (L_P, L_N, TP, TDP, and TN concentrations) and algal standing stocks (phytobiomass and chlorophyll *a*) and primary productivity (P = 0.01). Light extinction rates and pH were positively and CO_2 concentration negatively correlated with biomass and primary productivity as well. However, it is likely that for these relationships, the independent variables were the biological factors.

A large number of highly significant (P = 0.01) relationships between the relative (percentage of total) or absolute biomass of the algal groups and environmental variables were found. Correlated with cyanobacterial biomass (both absolute and relative) were chlorophyll *a* concentration, C fixation rate, various N fractions, pH, and CO_2 (the last in a negative fashion). For the Lake 302S portion of the data set, cyanobacterial biomass and relative biomass also were related to TP concentration, but in Lake 303, the same relationships were negative. Chlorophyte biomass and relative biomass also correlated with phytobiomass, C fixation rate, pH, CO_2 concentration (negative), and, in Lake 302S, TP concentration. Again, the relationship between biomass and TP concentration was negative in Lake 303.

Cryptophyte relative biomass correlated positively with measures of P availability (L_P and TDP) and CO_2 concentration and negatively with the percentages of cyanobacteria and chlorophytes in the phytoplankton. The absolute biomass of the group was not strongly related to P availability but was affected positively by CO_2 and DIC concentrations and negatively by pH. In Lake 302S, cryptophytes were prevalent, while biomass and productivity were relatively low, whereas in Lake 303, cryptophyte relative biomass increased with total phytoplankton biomass.

Chrysophytes were the most distinct group with regard to their response to environmental variables. Their biomass correlated positively with TN, DOC, DIC, and CO_2 concentration as well as with the TN:TP ratio and negatively with temperature, pH, and all measures of both P (L_P, TP, and TDP) and light availability. Relative biomass correlated with largely the same variables but was also negatively correlated with chlorophyll *a* concentration, total phytoplankton biomass, and primary productivity.

Canonical correlation analysis was done both with group biomass and group contribution to total biomass as variables and for the combined and lake-specific data sets. Table 3 shows the relationships obtained for the entire data set when the environmental variables were TP concentration, TN:TP ratio, pH, temperature, and average light intensity in the mixed layer. These variables were included either because Pearson product-moment correlation analysis revealed strong relationships with group biomass or because they were judged important by previous researchers. Substituting TN for TN:TP or CO_2 concentration for pH yielded very similar results (with pH and CO_2 concentration showing effects in opposite directions), as these factors were highly correlated. Two canonical variates with statistical significance were produced for both the relative and absolute biomass analyses. The first, more important, canonical variate for the relative biomass analysis indicated that cryptophytes were least important and nonheterocystous cyanobacteria most important when pH was high (or CO_2 concentration low). TN:TP ratio also contributed positively to the canonical variate but to a lesser extent than pH. The second canonical variate indicated that when TP concentration is high and pH more neutral (CO_2 concentration higher), chlorophytes, and especially cryptophytes, thrive. The canonical correlation for group biomass indicated in its first component that nonheterocystous cyanobacterial biomass is high and chrysophyte and cryptophyte biomass low when pH is high (CO_2 concentration is low) and in its second component that elevated nonheterocystous cyanobacterial and cryptophyte biomass is associated with high TN:TP ratios.

Because the analyses including all major phytoplankton

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divisions revealed little about the conditions favoring heterocystous cyanobacteria (the response of this group was obscured by the stronger responses of others), we performed an additional canonical correlation analysis in which the biomass of just nonheterocystous and heterocystous cyanobacteria was related to environmental variables. The results indicated that nonheterocystous cyanobacterial biomass was strongly associated with high TN:TP ratios and to a lesser extent with high temperatures and high TP concentrations (CV 1, Table 3), whereas heterocystous cyanobacteria were most abundant when TN:TP ratios were low, pH high, and light intensity subdued (CV 2). These three variables appeared to be roughly equal in their importance. That our two canonical correlations (with and without eucaryotes) suggested promotion of nonheterocystous cyanobacteria by somewhat different environmental factors was due to the fact that in one case, the group's preferences were distinguished from those of all algal groups, whereas in the other, only the factors distinguishing it from heterocystous cyanobacteria were determined.

Periphyton response to mesocosm fertilization

Wall periphyton biomass and productivity were measured to ensure that this group did not dominate resources in mesocosms and thus alter phytoplankton dynamics. No more than 25%, and generally <10%, of the total algal biomass in mesocosms was associated with wall growth (Tables 1 and 2). Periphyton biomass was at least twice as great in the N:P = 4 mesocosms as in neighboring N:P = 33 mesocosms, probably because these systems had lower phytoplankton biomass and thus greater light penetration. The periphyton present were principally diatoms early in the summer and chlorophytes later on (Levine 1983). Even in the N:P = 4 mesocosms with very low DIN concentrations, cyanobacteria were rare.

Epipelic and epipsammic algal biomass in the mesocosms was not monitored. However, it was visually clear that in littoral Lake 302S, the major algal response to fertilization at a low N:P ratio was the growth of periphyton mats over the sandy sediments. These mats were several centimetres thick and extended up the walls for half a metre or so in several places. The dominant alga in the mats was *Oedogonium* sp. The estimates of periphyton biomass in these mesocosms provided in Table 1 are unrealistically low, as they assume incorrectly that epipsammic algae formed a film on sediments as thin as that on mesocosm walls. Nevertheless, they indicate that >80% of the algae in the littoral N:P = 4 mesocosms were benthic.

Discussion

Heterocystous cyanobacteria and N:P ratios

Our experiments in mesocosms suggested that controls on cyanobacterial populations in ELA lakes are more complex than was immediately apparent in earlier whole-lake studies. Mesocosm fertilization at an N:P ratio of 33:1 yielded phytoplankton communities dominated by cryptophytes, chlorophytes, nonheterocystous cyanobacteria, and, in one case, chrysophytes, while heterocystous cyanobacteria were consistently scarce. However, fertilization at a lower N:P ratio (4.4:1) did not assure dominance by heterocystous cyanobacteria. In the Lake 303 mesocosms, none of these algae were seen, regardless of N:P supply ratio, while in Lake 302S's littoral N:P = 4 mesocosms, *Anabaena circinalis* and *Anabaena planktonica* appeared, but accounted for <1% of phytobiomass. Only in the pelagic N:P = 4 mesocosms of Lake 302S did heterocystous cyanobacteria gain dominance and create surface blooms, and this happened only after 6–8 weeks of mesocosm fertilization. Consequently, the experiments raised two important questions: (*i*) why were there no cyanobacterial blooms in littoral mesocosms and (*ii*) why, in the pelagic mesocosms, were blooms delayed until late summer?

Nutrient limitation in the mesocosms

ELA lake sediments recycle N more efficiently than P (Schindler et al. 1987; Levine and Schindler 1992). Because of this phenomenon and allochthonous inputs, mean L_N:L_P ratios for the N:P = 4 mesocosms were much greater than 4:1, from 8:1 to 24:1. Consequently, it is possible that cyanobacteria did not consistently respond to fertilization at a low N:P because N limitation was not consistently induced. To evaluate nutrient limitation type in mesocosms, we examined inorganic nutrient concentrations, primary productivity and phytobiomass. Phytoplankton exploit nutrients that limit their growth to the full extent possible while leaving unlimiting nutrients to accumulate in solution. Thus, two symptoms of N limitation are DIN concentrations near and orthophosphate (dissolved inorganic phosphorus (DIP)) concentrations well above analytical detection limits. DIP concentrations cannot be accurately measured in ELA lakes because the molybdate blue method cleaves substantial amounts of phosphate from dissolved organic compounds (Stainton 1980). However, we interpreted greater TDP concentrations in some mesocosms than in others as an indicator of possible DIP accumulation. Another manifestation of N limitation in lakes is lower phytoplankton standing stocks and rates of primary productivity per micromole of available P than in P-limited systems, due to incomplete P usage. Because our mesocosms received similar amounts of P fertilizer, productivity and biomass accumulation could be compared directly.

Three of the seven N:P = 4 mesocosms displayed multiple symptoms of N limitation: the one in Lake 303 with a plastic floor and the two littoral mesocosms of Lake 302S. In these mesocosms, mean DIN concentrations were close to the detection limit, 1 μM, while TDP concentrations were about twice the levels in mesocosms that received N and P at a ratio of 33:1. Phytobiomass, chlorophyll *a* concentrations, and primary productivity were at most one third of the standing stocks and rates in neighboring N:P = 33 mesocosms and insignificantly different from the values for the surrounding oligotrophic lakes. Mean L_N:L_P ratios for these mesocosms were between 13:1 and 17:1.

Phosphorus limitation in mesocosms fertilized at an N:P ratio of 33:1 also was readily apparent: DIN concentrations were substantial, TDP concentrations minimal, and mean phytobiomass and C fixation rates much greater than in the N:P = 4 mesocosms. In the remaining four N:P = 4 mesocosms, nutrient limitation appeared to be either mixed or variable over time. TDP accumulation was minimal in all, and in three of the four, DIN concentrations were near the detection limit (the exception was the mesocosm with the

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greatest L_N:L_P ratio, 24:1). Phytoplankton biomass and primary productivity rates were intermediate between those observed in the three more strictly N-limited mesocosms and those in the P-limited N:P = 33 mesocosms. This group of mesocosms, with mean L_N:L_P ratios between 8:1 and 24:1 and TN:TP ratios between 32:1 and 64:1, included the two pelagic mesocosms that eventually developed cyanobacterial blooms.

In conclusion, we believe that some degree of N deficiency occurred in all of the N:P = 4 mesocosms, although the one with a mean L_N:L_P ratio of 24:1 was principally P limited. N limitation was the rule in at least three mesocosms. Clearly, the scarcity of cyanobacteria in littoral mesocosms and their delayed appearance in pelagic mesocosms cannot be attributed to a lack of selection pressure for species efficient in N acquisition.

Nonheterocystous cyanobacteria and N:P ratios

Although Smith (1983, 1985) and others have proposed that nonheterocystous as well as heterocystous cyanobacteria are favored by low N:P ratios, our experiments did not support this contention. ANOVA, Pearson product-moment correlation analysis, and canonical correlation analysis all indicated that nonheterocystous cyanobacterial biomass in the mesocosms was positively rather than negatively correlated with L_N:L_P or TN:TP. Because *Oscillatoria*, *Lyngbya*, or *Pseudoanabena* have been frequent dominants or subdominants in ELA lakes fertilized at N:P ratios of 29:1 to 31:1 (Findlay 1981), we were not surprised by this outcome. Nor were our findings unique. In empirical analyses of 435 and 137 lakes, Harris (1986) and Canfield et al. (1989) found no relationship between overall cyanobacterial biomass and TN:TP ratios. *Anabaena* and *Aphanizomenon* were more abundant at low than at high N:P ratios, but the reverse was true for *Oscillatoria* and *Lyngbya*, and *Microcystis* was represented over most of the N:P range (Harris 1986). Lakes fertilized with N in an effort to eliminate *Anabaena* and *Aphanizomenon* have sometimes developed equally obnoxious blooms of *Microcystis* (Lean et al. 1978; Barica et al. 1980) or, in one case, dominance by the tiny cyanobacterium *Synechococcus* (Stockner and Shortreed 1988).

Assessment of optimal N:P supply ratios (ratios yielding maximum growth rates) for cyanobacteria in continuous cultures has confirmed that not every species is adapted to low-N conditions. Species averages ranged from 0.5:1 to 71:1 (Pick and Lean 1987, and references therein) and thus totally overlapped the reported range for eucaryotic species, 7:1 to 44:1 (Rhee and Gotham 1980). Clearly, the low-N:P theory of cyanobacterial dominance is appropriate only for N_2-fixing species.

Cyanobacteria and environmental factors other than N:P ratios

The lack of fidelity between the development of N-limiting conditions and the rise to dominance of heterocystous cyanobacteria in our mesocosms suggested that there are factors besides N:P ratio that affect cyanobacterial growth. We used the physicochemical data that we gathered to assess the validity of various hypotheses in the literature that explain cyanobacterial dominance on the basis of factors other than, or in addition to, N:P ratios. McQueen and Lean (1987) hypothesized that cyanobacterial dominance in Lake St. George, Ontario, required not just low N:P ratios (NO_3:TP < 11:1), but also warm temperatures (>21°C). Competition studies in the laboratory led Tilman and Kiesling (1984) to a similar conclusion: cyanobacteria dominated cultures only when temperatures were >24°C and DIN:TP ratios <9:1. During our experiments, temperatures were often <21°C, and thus perhaps unfavorable for cyanobacterial dominance. However, neither Pearson product-moment correlation nor canonical correlation analysis indicated any relationship between cyanobacterial abundance (or relative abundance) and temperature. Cyanobacteria gained dominance in pelagic mesocosms while the lake was cooling and continued to increase in numbers right up until fall overturn. Canfield et al. (1989) also found no relationship between cyanobacterial dominance and temperature in their 137 Florida lake data set.

Low light intensity is another variable that may encourage cyanobacterial dominance (Smith 1986; Klemer 1991). In general, cyanobacteria are able to grow at lower light intensities than eucaryotic species, and some have gas vesicles that allow them to rise to the surface and eliminate competitors through shading (Klemer 1991). Low light and low N:P ratios (or high TP concentration) may be cofactors in cyanobacterial selection, particularly since the optimal N:P supply ratios of algae appear to vary with light intensity (Rhee and Gotham 1981; Healey 1985). Smith (1985, 1986) and Smith et al. (1987) have found that multiple regression models most accurately predict cyanobacterial biomass when the variables include mixed layer and Secchi depths, factors that relate to light availability.

Canonical correlation analysis of the data from our study indicated that low light availability was one of three environmental conditions coincident with periods of high heterocystous cyanobacterial biomass. However, it was unclear whether low light played a role in bringing *Anabaena* to dominance. Light intensities seemed to track rather than precede gains in *Anabaena* biomass (Levine 1983), suggesting that algae were the independent variable in the relationship. Light availability was not an important canonical variate for the biomass of nonheterocystous cyanobacteria in mesocosms (none of which were scum formers).

High pH and low CO_2 concentrations are other environmental variables that may favor cyanobacteria over eucaryotic algae. Cyanobacteria have exceptionally low half-saturation constants for CO_2 uptake, are able to hydrolyze bicarbonate as a source of CO_2, can concentrate CO_2 prior to photosynthesis, thus elevating C fixation rates, and, when vacuolated, can migrate to the water surface to take advantage of the higher CO_2 concentrations at the air–water interface (Talling 1976; Paerl and Ustach 1982; Raven 1985). Canfield et al. (1989) found a significant positive relationship between cyanobacterial biomass and pH in 137 Florida lakes, and Smith et al. (1987) reported that *Aphanizomenon* dominance in Swedish lakes was most accurately predicted from multiple regression models that included DIC concentration as well as TP concentration and temperature. Cyanobacterial blooms have been eliminated from experimental mesocosms through addition of acid, CO_2, or bicarbonate (Shapiro 1990, and references therein, but also note that a lake bubbled with CO_2 remains dominated by cyanobacteria (Shapiro 1997)).

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ELA lakes have exceptionally low DIC concentrations. Consequently, when whole lakes or mesocosms in this region are fertilized, the increased productivity often results in highly elevated pH values (>9.0) and very low concentrations of CO_2. The diffusive flux of atmospheric CO_2 into ELA lakes is sufficient to permit eutrophication to proceed in proportion to P inputs, but C fixation rates frequently are limited by C availability during the afternoon (Schindler and Fee 1973). Both nonheterocystous and heterocystous cyanobacterial biomass correlated positively with pH and negatively with CO_2 concentration during our experiments. In CO_2-rich Lake 303, cyanobacteria were scarce, while in Lake 302S, succession from cryptophytes to cyanobacterial and chlorophyte dominance was coincident with rising pH and plunging CO_2 values. Thus, it is tempting to conclude that CO_2 concentration is the major variable controlling cyanobacterial biomass in ELA lakes and assign N:P ratio the role of selecting between heterocystous and nonheterocystous species once cyanobacteria are already favored. However, examination of pH, CO_2, and phytoplankton data from the past 30 years of whole-lake fertilizations at ELA indicated that low CO_2 and high pH have not always been preconditions for cyanobacterial dominance. In Lake 227, *Aphanizomenon* bloomed primarily during periods of high pH, but high pH did not guarantee their dominance. Many high-pH episodes favored chlorophytes (Findlay et al. 1994). In Lake 226 NE, *Anabaena* blooms frequently occurred at near neutral pH (ELA unpublished data).

Akinetes and their response to environmental cues also may have influenced cyanobacterial dynamics in our experimental mesocosms. A prerequisite for the testing of any hypothesis regarding cyanobacterial dominance is that the test organisms be present. Although nonheterocystous cyanobacteria were found in all Lake 303 mesocosms, not a single specimen of a heterocystous species was seen. Heterocystous species may not have colonized Lake 303, or benthic akinetes may not have germinated. In addition, the mesocosm that was most N limited had a plastic floor, which may have served as as an effective barrier to the immigration of sediment-derived cells. Lack of cyanobacterial dominance in the littoral mesocosms of Lake 302S cannot be explained on the basis of missing innoculum, however, as *Anabaena circinalis* and *Pseudoanabena catenata* were both present at low densities in late summer. Neither species was detected prior to late June, however. Therefore, it is possible that the timing of the cyanobacterial blooms in pelagic mesocosms was related to, or partly related to, seasonal factors affecting akinete germination.

One other factor potentially important to species selection was not measured during our study: zooplankton grazing. Cryptophytes and chrysophytes are believed to be particularly vulnerable to grazers, while cyanobacteria and large or mucilaginous chlorophytes are considered relatively immune (Haney 1987). A zooplankton sample taken from Lake 303 during our study indicated that grazer densities were very low (M. Patterson, Department of Fisheries and Oceans, Freshwater Institute, Winnipeg, Man., personal communication), probably because fathead minnows (*Pimephales promelas*) were abundant. Were zooplankton equally scarce in the mesocosms, the observed survival of high densities of edible *Rhodomonas* would be explained. Although we have suggested that plunging CO_2 concentrations were the major reason for the replacement of cryptophytes with chlorophytes and cyanobacteria in Lake 302S, we cannot dismiss the possibility that zooplankton densities rose in midsummer and cryptophytes were preferentially consumed. The literature suggests that zooplankton grazing exerts its greatest influence on phytoplankton communities when large daphnids dominate (Carpenter et al. 1985; Mazumder 1994), however, and these animals are uncommon in ELA lakes.

Environmental factors affecting eucaryotic algae

N:P ratio affected the maximum biomass achieved by the dominant phytoplankton group in each of the study lakes (cryptophytes in Lake 303 and chlorophytes in Lake 302S) but did not affect group relative abundance. A role for N:P ratio in structuring phytoplankton communities may have been obscured, however, by species aggregation into divisions. We observed different chlorophyte and cyanobacterial species dominants at high and low N:P fertilization ratios.

Canonical correlation analysis provided information on other physicochemical factors that may select between groups. For chrysophytes, dominance was associated with low TP concentrations, relatively high TN concentrations, pH near neutral, and an abundance of CO_2. This combination of conditions is normally found in ELA lakes, and chrysophytes generally dominate year-round. While chrysophytes are considered oligotrophic species (Sandgren 1988), they responded strongly to fertilization in one of our Lake 303 mesocosms. This mesocosm had L_N:L_P and TN:TP ratios greater than those of other mesocosms (suggesting high N availability) and existed over sediments producing substantial amounts of CO_2. Thus, it may be that N or C dynamics are more important than P in chrysophyte selection. Chrysophytes differ from many of the other phytoplankton groups in that they do not produce the exogenous carbonic anhydrase needed to use bicarbonate as a C source (Sandgren 1988). Thus, they require higher CO_2 concentrations.

Very little is known about the environmental requirements of cryptophytes (Klaveness 1988). Canonical correlation analysis on our data set, which included cryptophytes as frequent dominants, indicated that the group does well when TP concentrations are fairly high but pH remains near neutral and CO_2 is readily available. Cryptophytes thrived at both high and low TN:TP ratios but attained greater densities when ratios were high. Thus, cryptophytes and chrysophytes appeared to prefer similar conditions, but the former generally were found under more eutrophic conditions than the latter.

The Chlorophyta is a large group, highly diverse both taxonomically and in its physicochemical requirements (Happey-Wood 1988). It is not surprising, then, that we found chlorophytes in all of our experimental mesocosms, regardless of treatment or pH, and that canonical correlation analysis suggested only mild associations between chlorophyte biomass or relative biomass and environmental variables. Pearson product-moment analysis associated high chlorophyte biomass with the same group of variables encouraging cyanobacterial growth: high productivity and phytoplankton standing stocks, high pH, and low CO_2. Although adaptation to low CO_2 is generally considered strictly a cyanobacterial trait (Shapiro 1990), our study suggested that at least some

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chlorophyte species are tolerant of severe C scarcities; *Characiochloris incrassata* and three species of *Monoraphidium* (*M. dybouski*, *M. minutum*, and *M. contortum*) weathered several weeks of pH values >9 and CO_2 concentrations <0.2 μM.

Periphyton and N:P ratios

The development of mats of periphyton in the duplicate N:P = 4 mesocosms of littoral Lake 302S was a reminder that the resources that phytoplankton compete for may be subject to benthic demands as well. Which community predominants in shallow waters may be determined by resource limitation type and by how resources enter the system. In ELA lakes, sediments are a significant source of N but not of P. Thus, N limitation encourages algal growth near the sediment surface, where there is an efflux of ammonium, while P or light limitation favors planktonic species. That periphyton mats did not develop in Lake 303 may be related to the exceptionally high sediment N fluxes involved and to flocculent, easily stirred sediments. Enough N passed through epipelic communities in this lake to support elevated phytoplankton growth and the subsequent shading of periphyton at depth. In both lakes, periphyton growth on walls was thicker in low- than in high-N:P mesocosms of similar P supply. This was probably because phytoplankton biomass was greater at high N:P supply ratios and the periphyton thus more strongly shaded.

Results similar to ours were obtained when P, but not N, fertilizer was added to Lake Hymenaure, Sweden, and ELA Lake 261 (Persson et al. 1977; Schindler 1977, 1980). Periphyton growth increased markedly, while phytoplankton showed at best a mild growth response. In both lakes, N fixation occurred among the epilithon, but not within the epipelon (measured only in Lake Hymenaure), suggesting that the former lacked a reliable DIN source, while the latter did not. The mats formed in our mesocosms were composed of chlorophytes, not cyanobacteria adapted to low N availability.

Conclusions

It has been known for a century that lake trophic state affects phytoplankton composition, but the mechanisms of species selection are still under investigation. Our study suggests that rising pH and plunging CO_2 concentrations play a role in the elimination of chrysophytes and cryptophytes and the rise to dominance of cyanobacteria and chlorophytes during lake eutrophication. A strong role for N:P supply ratios in selecting between phytoplankton divisions was not apparent. However, species-level differences in treatment response were observed within divisions, the most striking being the positive response of *Pseudoanabaena* versus the negative response of *Anabaena* to rising L_N:L_P ratios. Traditionally, species succession is analyzed at the division level to reduce the labor involved and the chance of misidentifications. Our results suggest that species-level studies might be considerably more productive and also more meaningful, as selection is a population-level phenomenon.

Our findings have a number of management implications. They suggest that blooms of heterocystous cyanobacteria such as *Anabaena* and *Aphanizomenon* may be controlled through measures that raise N:P supply ratios, while blooms of nonheterocystous species such as *Microcystis* cannot. Therefore, we do not recommend N fertilization as a means of controlling cyanobacterial blooms. Nitrogen additions to lakes dominated by heterocystous species may result in a species shift towards *Microcystis*. Phosphorus input reductions remain the most effective means of cyanobacterial control, as both nonheterocystous and heterocystous cyanobacteria are favored by high P availability (also see Watson et al. 1997). Not all eutrophic lakes with low N:P supply ratios will develop cyanobacterial blooms. Those with sediments that are firm and that recycle substantial amounts of N may support periphyton mats instead. The interplay between phytoplankton and periphyton communities in shallow lakes deserves greater attention.

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Accumulation of Cd by a freshwater mussel (*Pyganodon grandis*) is reduced in the presence of Cu, Zn, Pb, and Ni

A.R. Stewart

Abstract: The effects of a metal mixture on Cd bioavailability and uptake in the freshwater mussel *Pyganodon grandis* (formerly *Anodonta grandis grandis*) were investigated in a limnocorral experiment in a Precambrian Shield lake during the summer of 1992. Differences in the partitioning of Cd in water, sediment, and mussels were identified between limnocorrals treated with Cd alone or with Cd and a mixture of metals (Cu, Zn, Pb, and Ni) at three concentration levels. Loss of Cd from the water column was slower in treatments with the metal mixture (22- to 34-day half-life) than in the treatment with Cd alone (11-day half-life). Despite the higher concentrations of Cd in the water column in treatments with the mixture of metals, the mussels accumulated proportionally less Cd as the metal concentrations increased. These relationships were observed in mussels exposed for 40 days ([Cd] <4.4 $\mu g \cdot L^{-1}$) and 80 days ([Cd] = 4–14 $\mu g \cdot L^{-1}$). The uncoupling of the effects of the metal mixture on Cd bioavailability and uptake suggests that laboratory studies may be appropriate for characterizing metal uptake in mussels exposed to mixtures of metals under nonequilibrium conditions. The significant deviation in the behavior of Cd in the presence of the metal mixture emphasizes the need to further investigate regulatory approaches that focus on individual contaminants.

Résumé : On a étudié les effets d'un mélange de métaux sur la biodisponibilité du Cd et l'absorption de ce métal par la moule d'eau douce *Pyganodon grandis* (anciennement *Anodonta grandis grandis*) dans le cadre d'une expérience en enceintes limnologiques menée dans un lac du Bouclier précambrien durant l'été de 1992. On a observé des différences dans la répartition du Cd dans l'eau, les sédiments et les moules entre l'enceinte dans laquelle on a introduit seulement du Cd et les enceintes dans lesquelles on a introduit du Cd et un mélange de métaux (Cu, Zn, Pb et Ni) à trois concentrations. La diminution de la concentration de Cd dans la colonne d'eau était plus lente dans les traitements utilisant le mélange de métaux (demi-vie de 22–34 jours) que dans le traitement utilisant le Cd seul (demi-vie de 11 jours). Malgré les plus fortes concentrations de Cd dans la colonne d'eau dans les traitements utilisant le mélange de métaux, les moules accumulaient proportionnellement moins de Cd quand on passait à une concentration de métaux supérieure. Ces relations ont été observées chez les moules exposées durant 40 jours ([Cd] <4,4 $\mu g \cdot L^{-1}$) et 80 jours ([Cd] = 4–14 $\mu g \cdot L^{-1}$). L'effet restrictif du mélange de métaux sur la biodisponibilité et l'absorption du Cd laisse penser que des études en laboratoire pourraient être utiles pour caractériser l'absorption des métaux par les moules exposées à des mélanges de métaux dans des conditions non équilibrées. La modification significative du comportement du Cd en présence du mélange de métaux met en lumière la nécessité de réviser les méthodes de réglementation qui considèrent les contaminants individuellement.

[Traduit par la Rédaction]

Introduction

In the environment, contaminants are generally present as mixtures. For example, toxic heavy metals from nonferrous metal mining, smelting, and refining processes are released together into aquatic ecosystems through atmospheric deposition, surface runoff, and milling effluents (AQUAMIN 1996; Nriagu 1990). The resulting mixture of heavy metals in the receiving waters may interact and mutually influence metal toxicity in aquatic organisms. Metal mixture toxicity has been shown to deviate from that expected for individual metals for numerous species tested in the laboratory (Voyer and Heltshe 1984; Spehar and Fiandt 1986; European Inland Fisheries Advisory Commission 1987; Keller and Zam 1991; Kraak et al. 1994). Virtually nothing is known about metal mixture toxicity in the field.

Metal toxicity in nature is determined to a great extent by the availability of individual metals for uptake by organisms. In the aquatic environment, metal transport, partitioning, and bioavailability are determined by a host of physicochemical factors including organic matter, redox potential, pH, and substrate type. Metal mixtures may also influence metal bioavailability, depending on metal concentrations, relative binding strengths of the metals for various substrates (K_d or partitioning coefficient), and the physiological roles of the metals. Metals introduced into surface waters are eventually lost to and accumulate in the sediment. Transport to the sedi-

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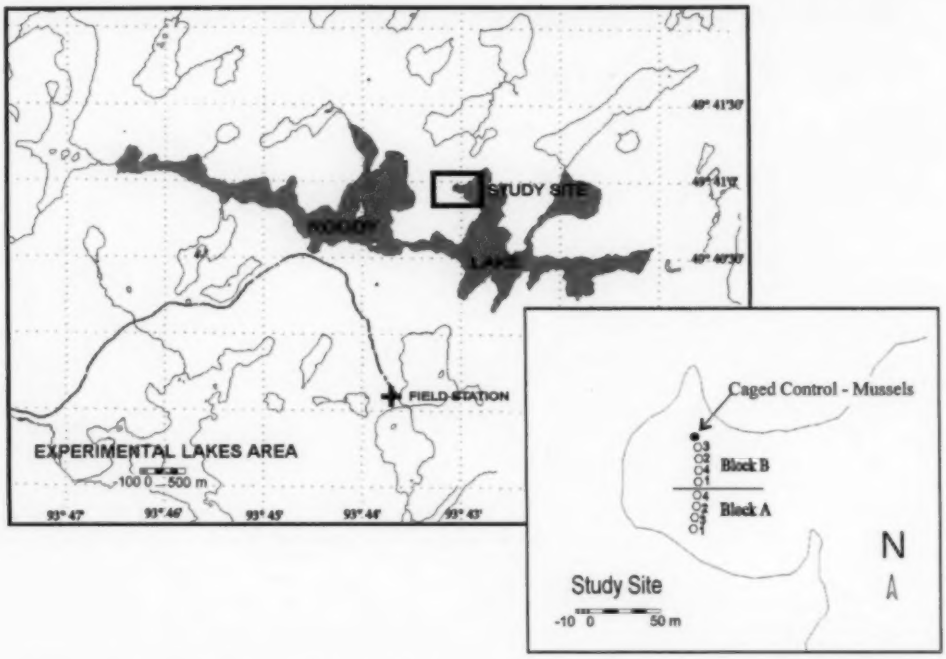
Fig. 1. Location of study site in Roddy Lake at the Experimental Lakes Area. Locations of limnocorrals and treatment assignment between blocks are also shown.



ment can occur by metals adsorbing onto settling particles in the water column or by metals directly adsorbing onto particles at the sediment–water interface (Luoma 1983; Santschi et al. 1986; Campbell and Tessier 1996). It is hypothesized that in the presence of large quantities of metals such as in mining or industrial effluents, binding sites on particles may become limiting, thus influencing the removal of metals from the water column. Metals remaining in the water column can be accumulated by phytoplankton, zooplankton, filter-feeding macroinvertebrates, and fish (Morel 1983; Campbell and Tessier 1996). If metal mixtures influence the bioavailability of metals in the water column, then corresponding changes in tissue metal concentrations would be expected. Field studies representing the complexity of natural processes are needed to elucidate the behavior of metal mixtures, their effect on the bioavailability of metals in natural systems, and consequently their toxicity to aquatic organisms.

To investigate the effects of a metal mixture on Cd bioavailability, differences in the partitioning of Cd in water, sediment, and the freshwater floater mussel *Pyganodon grandis* (Say) Hoeh (formerly *Anodonta grandis grandis*) were identified between limnocorrals treated with Cd alone or with Cd and a mixture of metals (Cu, Zn, Pb, and Ni) at three concentration levels. The experiment was conducted in a lake at the Experimental Lakes Area (ELA), northwestern Ontario. Cadmium, a priority substance under the Canadian Environmental Protection Act, is highly toxic to aquatic organisms and is commonly released with the metals Cu, Zn, Pb, and Ni during mining, smelting, and other industrial processes (Nriagu 1990). *Pyganodon grandis* is useful in assessing the bioavailability of metals in contaminated environments (Couillard et al. 1993, 1995; Tessier et al. 1993; Malley et al. 1995; Stewart 1997). Limnocorrals were dosed so that the resulting sediment metal concentrations were in the range of sediment concentrations found in lakes near base-metal smelters (Harrison and Klaverkamp 1990). The aim of this study was to determine if metal mixtures affect the bioavailability of Cd in the aquatic environment and whether or not the resulting environmental metal concentrations can be used to explain tissue metal concentrations. Conclusions of this field study are used to evaluate the relevance to natural systems of metal mixture studies conducted in the laboratory.

Methods

Experimental site

The ELA is located 52 km southeast of Kenora, Ontario, on the southwestern part of the Precambrian Shield (Brunskill and Schindler 1971). The ELA comprises some of the most oligotrophic lakes in the world. They are representative of small lakes especially prone to acidification and contamination from metals and organic pollutants (Schindler 1988). Apart from small-scale logging in previous years, limited fishing and hunting, past occurrence of forest fires, and regional LRTAP deposition, the ELA remains pristine.

The site of the limnocorral experiment was a shallow, protected bay in Roddy Lake (93°43'W, 49°41'N) (Fig. 1). Water chemistry for Roddy Lake is shown in Table 1. The experimental site consisted of littoral sediment composed of sand and gravel (1–2% loss on ignition) down to a depth of 6–8 cm, below which there was clay. There was a slight gradient of increasing sedimentary organic matter (~10% difference) from north to south along the transect where the limnocorrals were situated. The bay contained isoetid

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Table 1. Surface water chemistry of Roddy Lake and Lake 104.

Parameter	Roddy Lake	Lake 104
NH_4-N ($\mu g \cdot L^{-1}$)	9.7±4.0	9
Dissolved inorganic carbon ($\mu mol \cdot L^{-1}$)	143±8	120
Dissolved organic carbon ($\mu mol \cdot L^{-1}$)	413±23	940
Na ($mg \cdot L^{-1}$)	1.00±0.05	0.98
K ($mg \cdot L^{-1}$)	0.43±0.07	0.44
Ca ($mg \cdot L^{-1}$)	2.41±0.12	2.53
Mg ($mg \cdot L^{-1}$)	0.68±0.02	0.68
Fe ($mg \cdot L^{-1}$)	0.02±0.01	0.14
Mn ($mg \cdot L^{-1}$)	0.01±0.0	0.01
Cl ($mg \cdot L^{-1}$)	0.37±0.02	0.24
SO_4 ($mg \cdot L^{-1}$)	3.23±0.09	1.64
Alkalinity ($\mu equiv. \cdot L^{-1}$)	134±4.7	123
pH	6.74–7.27[a]	6.59
O_2 ($mg \cdot L^{-1}$)	9.15±0.41	8.7

Note: Values for Roddy Lake are means ± SD of six samples from 8 June to 15 October 1992. Values for Lake 104 are based on a single sample taken on 15 September 1992.
[a]Range.

macrophytes including *Eriocaulon septangulare* and *Juncus* sp. and a few resident *P. grandis*.

Experimental design

The experiment consisted of four duplicate treatments ($n = 2$) for a total of eight limnocorrals (Fig. 1). Treatments 1–4 received Cd additions targeted to raise sediment Cd concentrations by seven times above background (Table 2). Treatments 2–4 also received a mixture of Cu, Zn, Pb, and Ni to raise sediment Cu, Zn, Pb, and Ni concentrations by three, four, or seven times above background, respectively (Table 2). To compensate for the small gradient in organic matter that could affect metal bioavailability and confound the results, a randomized block ANOVA design was used. Each treatment duplicate was randomly assigned within a southern block (A, lower organic matter) and a northern block (B, higher organic matter) (Fig. 1). This experimental design reduced the chance that statistical differences among treatments were the result of the gradient in organic matter rather than a treatment effect (Hurlbert 1984). No statistically significant differences between the two blocks were found ($P > 0.05$) in metal concentrations in water, sediments, or mussels.

Mussels were introduced into the eight limnocorrals 3 weeks after the metal additions to the limnocorrals were completed and when metal levels in the water column were still high. A second group of mussels was introduced after 40 days when metal levels were low to compare responses to two exposure levels. Additional mussels were introduced into a cage outside the limnocorrals on days 0 and 40 to serve as transplant controls (Fig. 1). The cage was open to the sediment and was composed of plastic mesh (1 cm in diameter, 250-cm-high borders), allowing unrestricted exposure of the mussels to lake water. The aquatic macrophyte *E. septangulare* was also introduced into the limnocorrals on day 0. The accumulation of metals in *E. septangulare* will be described elsewhere.

The limnocorrals were 2-m-diameter cylindrical tubes about 1.5 m deep, composed of impermeable, reinforced woven translucent plastic (Curry Industries, Winnipeg, Man.). At the lake surface, the limnocorrals were supported by styrofoam floats, each in a reinforced vinyl pocket closed with plastic ties and supported by an external aluminum frame. The bottom of the limnocorrals ended in skirts that extended outward onto the sediment surface and were secured on the sediment with sandbags placed by snorkel divers.

Metals as salts ($CdCl_2 \cdot 2.5H_2O$, $CuCl_2 \cdot 2H_2O$, $ZnCl_2$, $Pb(NO_3)_2$, and $NiCl_2 \cdot 6H_2O$; Fisher Scientific Co., Winnipeg, Man., ACS grade) dissolved in 1 L of deionized distilled water were added to limnocorrals in five separate additions on 5, 16, 17, 19, and 22 June 1992. The exposure experiment began on 13 July 1992 (day 0), 3 weeks after the final metal addition. Chloride samples were taken weekly from the limnocorrals and Roddy Lake beginning 15 July 1992 until the end of the experiment to monitor the limnocorrals for leakage. Because most of the metals were added as chloride salts and Cl^- does not adsorb onto particulates or sediment, Cl^- levels should have remained elevated at a constant concentration above the ambient lake water level. From the time of final metal addition until day 80, Cl^- levels in the treatments decreased by about 2–12%, after adjusting for changes in limnocorral water volume due to precipitation and evaporation. This amount of leakage is less than that observed in other ELA limnocorral experiments (Santschi et al. 1986).

Table 2. Experimental design.

	Treatment			
Metal	1	2	3	4
Cd	7×	7×	7×	7×
Cu	1×	3×	4×	7×
Zn	1×	3×	4×	7×
Pb	1×	3×	4×	7×
Ni	1×	3×	4×	7×

Note: Values are the factors by which sediment metal concentrations were targeted to be increased above background. Each treatment was represented by two limnocorrals.

Collection and deployment of mussels

The source of *P. grandis* introduced into the limnocorrals was Lake 104 (93°50′W, 49°41′N). Lake 104 is a brown-water lake with higher dissolved organic carcon and slightly lower pH than Roddy Lake (Table 1). Transplantation of the mussels to Roddy Lake did not expose them to an appreciable change in water quality. On day 0 (13 July) and day 40 (27 August), 180 and 25 mussels, respectively, of about 9 years of age and 10 ± 0.8 cm in length (mean ± SD) were collected by snorkel divers and transported in coolers to Roddy Lake. These mussels were introduced into the limnocorrals and control cage. Mussels were free to move within the limnocorrals and the cage. Mussels were also collected from Lake 104 on days 0, 40, and 80 (15 October) for background metal determinations.

Water and sediment sampling

To monitor the loss of metals from the water column, water samples were collected from Roddy Lake and limnocorrals in acid-washed polyethylene Nalgene bottles every 2 days from 5 June 1992 to 28 July 1992 and once a week thereafter until the experiment was terminated on 15 October (day 80). Total water samples (unfiltered) were acidified (0.5% HNO_3 Baker analyzed for trace metal analysis) immediately upon returning to the laboratory. The partitioning of metals in the water column of Roddy Lake and limnocorrals on days 0, 40, and 80 was determined in water samples drawn from 1 m depth using a peristaltic pump. The 1-m water samples were filtered through acid-washed 10-μm nylon mesh netting into a acid-washed Nalgene carboy to avoid clogging of the 1-μm filter; >10-μm particulates were discarded. At the field laboratory, the remaining water (~2.5 L) was filtered through a 1-μm-mesh, 142-mm-diameter polycarbonate membrane filter (Poretics Corp., Mississauga, Ont.) using acid-washed tubing and a vacuum pump. Samples of the <1-μm filtrate and a laboratory blank of 1-μm-filtered deionized distilled water were taken. The 1-μm laboratory blanks ($n = 3$) were all below the analytical detection limit

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for each metal (Cd, <0.02 $\mu g \cdot L^{-1}$; Cu, <0.5 $\mu g \cdot L^{-1}$; Zn, <0.5 $\mu g \cdot L^{-1}$; Pb, <0.3 $\mu g \cdot L^{-1}$; Ni, <0.5 $\mu g \cdot L^{-1}$). A 1-μm mesh was chosen rather than the commonly used 0.45 μm because the 1-μm cutoff is closer to the particle size retained by filter-feeding unionid bivalves. Analysis of stomach contents suggests that the smallest particle size retained by *Pyganodon* species is 8 μm in diameter (Tankersley and Dimmock 1993). Furthermore, the ELA Chemical Laboratory uses a mesh size of 1 μm to operationally define suspended and dissolved fractions.

Additional water samples were taken from Roddy Lake and limnocorrals 1A, 2B, 3A, and 4B once a month in June, July, August, and September for analysis of major ions (Na, K, Ca, Mg, Fe, and Mn), pH, alkalinity, dissolved organic carbon, dissolved inorganic carbon, sulfate, and oxygen. Chemical analyses were performed using methods from Stainton et al. (1977) with the following modifications. Dissolved organic carbon samples were analyzed by a heated persulfate digestion followed by total carbon analysis (total carbon analyzer model 700, OI Corp. College Station, Tex.) and dissolved inorganic carbon was measured using infrared detection of carbon dioxide.

To determine if target levels were achieved in limnocorral sediments, metal concentrations were measured in sediments on days 0, 40, and 80. Samples were collected from each limnocorral in triplicate with a 5-cm internal diameter plexiglass coring tube. The top 2 cm of the core was placed in an acid-washed centrifuge tube and centrifuged at 4000 rpm for 30 min to remove porewater. Sediments were then frozen at –30°C until analyzed for metals.

Sampling and processing of mussels

On day 80, mussels were collected from the limnocorrals by SCUBA divers, placed in polypropylene bags, and transported to the field laboratory for processing. Mussels introduced into the limnocorrals or control cage on day 0 and removed on day 80 were designated 0- to 80-day mussels, and mussels introduced on day 40 and removed on day 80 were designated 40- to 80-day mussels. Of the 205 mussels introduced into the limnocorrals and cage, six died (three from limnocorral 4B) and 30 mussels were not recovered until the following spring. The spring mussels were not included in the following analyses. Mussels were maintained without water at 7.5 ± 0.5°C (lake temperature on day 80) until they were processed within 12 h. No specific attempt was made to clear gut contents, since previous metal uptake experiments carried out at the ELA showed that gut clearing had little effect on whole-body or tissue contents of Cd (Malley et al. 1989).

Mussels were blotted dry and their shell length, height, thickness, and live weight were measured. There were no significant differences ($P > 0.05$) in mussel length, height, depth, and live weight among groups in the limnocorrals or cage. Mussels were removed from the shells and whole bodies were frozen in Whirl-pak bags or they were dissected into mantle, gill, foot, kidney, and remainder of body, i.e., viscera. Mussel shells and bodies were freeze-dried (Lab Con Co. Freeze Dry 5, Fisher Scientific Co., Winnipeg, Man.) and condition of the mussels was determined by the ratio of freeze-dried (fd) body weight to freeze-dried shell weight after Davenport and Chen (1987):

$$\text{Condition} = \frac{\text{fd body wt (g)}}{\text{fd shell wt (g)}}.$$

With few exceptions, mussels bearing glochidia were not included in the statistical analyses; the mass of glochidia in the gill can potentially confound comparisons of metal concentrations, which are calculated on a per weight basis. Whole-body metal concentrations were determined for 0- to 80-day and 40- to 80-day mussels from each limnocorral and for the cage (five animals per limnocorral or cage). Tissue metal concentrations were also determined for 0- to 80-day mussels from limnocorrals 1A, 2B, 3A, and 4B (four or five animals) and the cage (two animals). Background metal concentrations were determined for the whole bodies of Lake 104 mussels on days 0, 40, and 80 (minimum of six animals) and in individual tissues on day 80 (three animals).

Analysis of water, sediment, and tissues

Total water samples and <1-μm filtrate were analyzed for metals by graphite furnace atomic absorption spectrometry (GFAAS) and flame atomic absorption spectrometry (FAAS) on a Varian GTA-95 (Varian Instruments, Georgetown, Ont.). Precautions were taken to prevent contamination by soaking all glassware in concentrated HNO_3 (reagent grade) and rinsing it three times in deionized distilled water.

Sediments were freeze-dried, digested by Aqua Regia (4:1 HCl–HNO_3, reagent grade), and extracts analyzed for metals using FAAS and GFAAS. Duplicate samples (~100 mg) of National Research Council of Canada reference sediments MESS-1 and PACS-1 were analyzed with almost every sample run. Mean (micrograms per gram dry weight ± SD, n = 4–6) metal concentrations obtained here for the reference materials were within the range specified for certified values (given in parentheses): Cd, 2.47 ± 0.2 (PACS-1, 2.38 ± 0.2); Cu, 22.2 ± 1.8 (MESS-1, 25.1 ± 3.8); Zn, 161 ± 6.4 (MESS-1, 191 ± 17); Pb, 29.7 ± 4.4 (MESS-1, 34.0 ± 6.1); Ni, 42.0 ± 3.6 (PACS-1, 44.1 ± 2.0). Variability (coefficient of variation (CV)) among triplicate cores from individual limnocorrals for the different metals was follows: Cd, ~15%; Cu, ~20%; Zn, ~15%; Pb, ~21%; Ni, ~21%. All sediment concentrations were expressed on a dry weight basis unless otherwise specified.

Freeze-dried mussel bodies and tissues were ground in a coffee grinder for at least 15 s. Tissues were then digested using concentrated HNO_3 and an H_2O_2 oxidation step according to Malley et al. (1989). Metal concentrations were measured with FAAS and GFAAS using a Varian GTA-95 or polarized Zeeman Z-8200 with Zeeman background correction (Hitachi Scientific Instruments, Rexdale, Ont.). Duplicate samples of National Research Council of Canada reference materials Dolt-2 and Dorm-1 (~100 mg) were analyzed with every set of mussel samples. Measured Cd, Cu, and Zn concentrations in reference materials varied little over time (CV = 3–11%, n = 7–16) and were within the specified ranges for each metal. Lead and Ni concentrations in reference materials were more variable (CV = 18–45%, n = 10), but their means were within the certified ranges. Average CV's for whole-body metal concentrations calculated using replicate mussels within each limnocorral were as follows: Cd, 18%; Cu, 21%; Zn, 16%; Pb, 28%; Ni, 27%. The variations in metal concentrations of individual tissues were generally 1.5–2 times higher than the above CV's. The above CV's for whole bodies were similar to those reported in other field studies with *P. grandis* (Couillard et al. 1993). All whole-body and tissue metal levels were expressed on a dry weight basis unless otherwise specified.

Calculations and statistics

The loss rate for Cd from the water column in the different treatments was calculated as a half-life by fitting an exponential decay curve:

$$b = \frac{\ln C_0 - \ln C_t}{t}$$

$$t_{1/2} = \frac{\ln 2}{b}$$

where b is the loss rate coefficient, C_0 is the initial total water metal concentration, C_t is the final total water metal concentration, and t is the number of days between C_0 and C_t. The loss rate coef-

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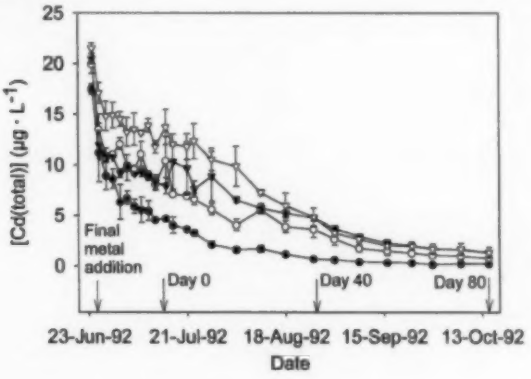
Fig. 2. Loss of Cd from the water column after the final metal addition. Values are means ± SE concentrations for each treatment (n = 2). Treatment 1 (solid circles), 11-day half-life; treatment 2 (open circles), 25-day half-life; treament 3 (solid triangles), 34-day half-life; treatment 4 (open triangles), 33-day half-life. Half-lives are calculated by fitting an exponential decay curve ($b = (\ln C_0 - C_t)/t$, where b is the loss rate coefficient, C_0 is the initial total water metal concentration, C_t is the final total water metal concentration, and t is the number of days between C_0 and C_t).



ficient for the exponential decay curve was optimized through a series of iterations using SigmaPlot version 4.0 (SPSS Inc. 1997).

Apparent partitioning coefficients, K_d^a, for Cd on particulate material and sediment were calculated for days 0, 40, and 80 according to Wood et al. (1995):

$$\text{Particulate } K_d^a = \frac{c_p}{c_f c_{ss}}$$

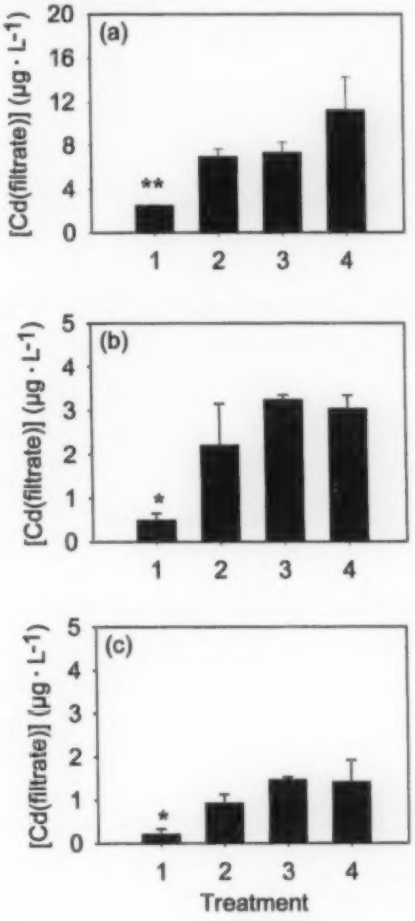
$$\text{Sediment } K_d^a = \frac{c_s}{c_f c_{ss}}$$

where c_p is the concentration of Cd adsorbed onto >1-µm particles (moles per kilogram), which is equal to the Cd concentration in the total water sample ([Cd(total)]) minus the Cd concentration in the 1-µm filtrate ([Cd(filtrate)]), c_s is the concentration of Cd in sediments (moles per kilogram of dry sediment), c_f is [Cd(filtrate)] (moles per kilogram), and c_{ss} is the concentration of suspended solids (milligrams per litre). Partitioning coefficients were termed "apparent", since the system was not in equilibrium.

The Cd body burden or "content" for mussel whole bodies and tissues was calculated as Cd body burden (micrograms) = Cd concentration (micrograms per gram dry weight) × body or tissue weight (grams dry weight).

Data were tested for normality using the Shapiro–Wilk statistic, a ratio between the best estimator of the variance and the corrected sum of squares estimator of the variance, and log transformed when required. Statistically significant differences in mussel size and metal concentrations in water, particulate material, and mussels among treatments were determined using SAS version 6.08 ANOVA, randomized blocks design (SAS Institute Inc. 1989). Differences in mussel condition and background tissue metal concentrations among Lake 104, the cage, and the treatments were also tested using ANOVA.

Fig. 3. Cd concentration in filtered water samples (<1 µm) at (*a*) day 0, (*b*) day 40, and (*c*) day 80. Values are means ± SE (n = 2). Treatment 1 is significantly different from the other treatments at $^*P < 0.05$ and $^{**}P < 0.01$.



Results

Loss of Cd and other metals from the water column

Cadmium remained in the water column longer in treatments with the metal mixture than with Cd alone (Fig. 2; Table 3). The half-life for Cd in treatment 1 was 11 ± 1 days (mean ± SE) compared with 25 ± 2, 34 ± 5, and 33 ± 3 days for treatments 2, 3, and 4, respectively. Water column [Cd(total)] in treatment 1 was significantly less than in treatments with the metal mixture on days 0 ($F_{3,3}$ = 19.97, P = 0.02) and 40 ($F_{3,3}$ = 40.54, P = 0.006) but not on day 80 (Table 3). As expected, Cu, Zn, Pb, and Ni concentrations in the water column of treatments 2–4 increased with increasing concentration of the metal mixture and declined with time (Table 3). Non-Cd metal concentrations in treatment 1 generally were indistinguishable from background concentrations as represented by Roddy Lake values (Table 3).

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Table 3. Metal concentrations ($\mu g \cdot L^{-1}$) in unfiltered water on days 0, 40, and 80.

	Day	pH	Cd	Cu	Zn	Pb	Ni
Roddy Lake	0	7.13	<0.02	<0.5	0.63	<0.3	<0.5
Treatment 1	0	6.89	4.61±0.02	<0.5	3.82±2.06	<0.3	<0.5
Treatment 2	0	7.04	9.30±0.87	11.9±1.6	128±8	29.9±5.4	18.5±0.7
Treatment 3	0	6.82	7.95±0.81	17.4±1.0	209±14	46.3±1.8	24.6±0.7
Treatment 4	0	6.78	13.7±1.7	30.8±0.6	414±4	87.0±2.0	56.7±5.4
Roddy Lake	40	7.27	<0.02	<0.5	1.55	0.52	<0.5
Treatment 1	40	7.33	0.66±0.14	<0.5	1.19±0.08	<0.3	<0.5
Treatment 2	40	7.02	3.20±0.63	4.55±0.47	38.0±5.4	4.38±0.62	6.15±1.06
Treatment 3	40	7.49	4.34±0.17	6.7±0.34	78.9±2.7	7.41±0.57	12.5±0.8
Treatment 4	40	7.56	4.00±0.17	10.7±0.4	155±21	12.1±1.5	21.9±0.7
Roddy Lake	80	6.74	<0.02	0.72	1.4	0.93	<0.5
Treatment 1	80	7.49	0.71±0.02	<0.5	2.50±1.69	<0.3	<0.5
Treatment 2	80	6.77	1.02±0.09	2.97±0.06	23.4±1.1	1.30±0.003	4.03±0.31
Treatment 3	80	7.59	1.66±0.03	4.12±0.17	47.6±1.0	1.68±0.26	7.59±0.23
Treatment 4	80	7.43	1.60±0.50	5.19±0.74	82.6±19.3	2.49±0.95	11.2±1.6

Note: Values are means ± SE (n = 2), except pH (n = 1).

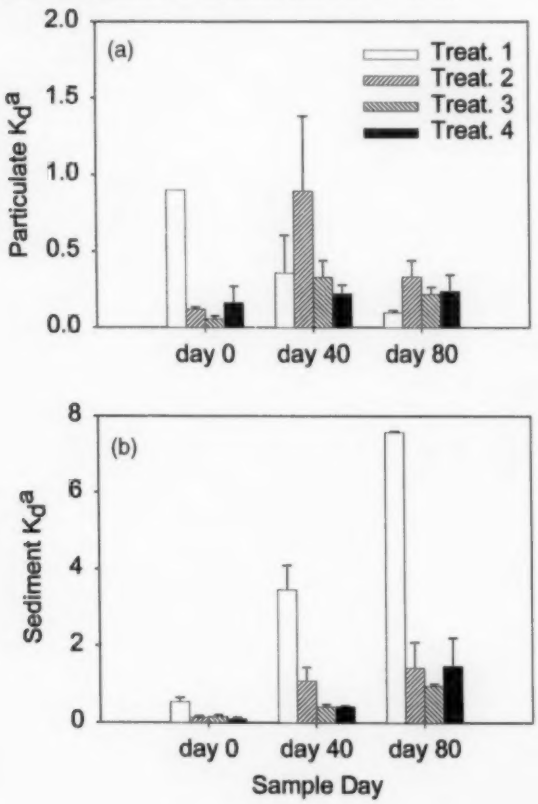

Fig. 4. (*a*) Particulate (>1 μm) and (*b*) sediment apparent partitioning coefficients for Cd in the limnocorrals on each sample day. Partitioning coefficients are calculated as ratios of the Cd concentration adsorbed onto particles or sediment to [Cd(filtered)]. Particulate partitioning coefficients are corrected for the concentration of suspended solids in the water.

The trends in the Cd concentration in the <1-μm filtrate ([Cd(filtrate)]) among treatments (Fig. 3) were similar to those for [Cd(total)] (Table 3) on each sample day. Values for [Cd(filtrate)] were significantly higher in treatments with the metal mixture compared with those in treatment 1 on days 0 ($F_{3,3} = 32$, $P < 0.01$), 40 ($F_{3,3} = 13$, $P < 0.05$), and 80 ($F_{3,3} = 13$, $P < 0.05$) (Fig. 3).

The trends in apparent partitioning coefficients for Cd on particles (K_d^a) (Fig. 4*a*) were less clear than those for the sediment K_d^a (Fig. 4*b*). The particulate K_d^a for treatment 1 progressively decreased from day 0 ($c_p = 0.087$, $c_f c_{ss} = 0.097$) to day 80 ($c_p = 0.001$, $c_f c_{ss} = 0.014$), corresponding to the loss of Cd from the water column to the sediments over the same time period (Fig. 4*a*). On day 0, particulate K_d^a in treatment 1 was considerably larger than those in treatments 2–4, but by day 40 was similar to those in treatments 3 and 4 that had increased from day 0. At the same time, treatment 2 particulate K_d^a was somewhat elevated above those in all other treatments, although its standard error was quite high. By day 80, values of particulate K_d^a in treatments 2–4 were larger than that in treatment 1. The K_d^a for the sediment in treatment 1 was consistently larger than those in treatments 2–4 and increased over time (Fig. 4*b*). This is consistent with the greater loss of Cd from the water column, represented by a smaller half-life (Fig. 2), and its sorption onto the surface sediment in treatment 1 relative to treatments 2–4.

Metal concentrations in sediments

Cadmium concentrations in limnocorral sediments reached target concentrations by day 0 in treatment 1 and by day 40 in treatments 2 and 3 but not until day 80 in treatment 4 (Table 4). Target concentrations of the other metals were reached in the sediments by 40 or 80 days (Table 4). Nickel concentrations in all treatments were slightly below target levels, and Pb concentrations in treatment 3 and 4 limnocorrals exceeded target levels. Unexpectedly, all of the metals were elevated in limnocorral 2A on day 40 relative to day 80.

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Table 4. Metal concentrations in limnocorral sediments on days 0, 40, and 80 compared with background sediment metal concentrations in Roddy Lake (background) and target metal concentrations.

			Metal concentration (μg·g dry weight^{-1})			
Metal	Background	Treatment	Target	Day 0	Day 40	Day 80
Cd	0.2±0.03	1	1.5	1.4±0.1	1.7±0.1	1.8±0.03
		2	1.5	1.0±0.1	2.1±0.2	1.4±0.2
		3	1.5	1.1±0.1	1.4±0.1	1.4±0.02
		4	1.5	1.0±0.1	1.3±0.1	1.7±0.2
Cu	0.6±0.07	1	Background	0.7±0.2	0.7±0.05	0.9±0.1
		2	1.6	1.0±0.2	1.7±0.3	1.4±0.4
		3	2.2	1.1±0.1	1.8±0.1	2.1±0.2
		4	3.8	1.9±0.2	3.2±0.3	3.6±0.6
Zn	5.3±0.8	1	Background	7.5±0.2	6.6±0.2	6.3±0.9
		2	16	11.1±1.2	18.0±2.1	12.3±2.9
		3	21	13.7±1.4	18.5±0.8	20.3±1.1
		4	37	17.3±1.0	27.2±2.0	34.3±4.5
Pb	1.8±0.04	1	Background	1.5±0.1	2.0±0.2	1.9±0.1
		2	5.4	3.6±0.3	9.5±1.4	5.3±1.6
		3	7.2	5.3±0.8	9.0±0.6	10.2±1.8
		4	13	9.3±1.6	17.3±1.1	23.1±5.6
Ni	1.0±0.4	1	Background	0.9±0.04	1.0±0.1	1.3±0.2
		2	3.1	1.9±0.3	2.9±0.7	2.5±0.7
		3	4.1	1.8±0.3	3.3±0.2	3.8±0.2
		4	7.2	2.5±0.3	4.6±0.3	6.5±0.9

Note: Values are means ± SE.

Table 5. Condition indices of mussels collected in October 1992 from the treatments and cage in Roddy Lake and source Lake 104.

	Condition index		
	Fresh, day 80	40–80 days	0–80 days
Lake 104	0.183±0.03	—	—
Cage	—	0.182±0.03	0.168±0.01
Treatment 1	—	0.179±0.01	0.129±0.01
Treatment 2	—	0.155±0.01	0.146±0.01
Treatment 3	—	0.189±0.02	0.146±0.004
Treatment 4	—	0.193±0.01	0.127±0.01

Note: Values for Lake 104 and the cage are means ± SE of five or six animals each. Values for treatments are means of replicate treatments consisting of means of five animals in each.

Condition of the mussels

Transplanting mussels from Lake 104 to the cage in Roddy Lake for 80 days did not significantly affect condition. Mussels collected from the cage in Roddy Lake in October had a condition index of 0.168, which was not significantly different from the condition index of 0.183 for mussels freshly collected from Lake 104 in October (Table 5). Enclosure in the limnocorrals for 80 days relative to caged mussels in Roddy Lake, nevertheless, was associated with a decline in condition in treatments 1 and 4 but not in treatments 2 and 3 ($F_{5,1} = 11$, $P = 0.04$) (Table 5). This difference between mussels in the limnocorrals and the cage was not seen in the 40- to 80-day mussels. The longer the mussels were held in the limnocorrals, the lower their condition. For example, 0- to 80-day mussels in treatment 4 were lower in condition than 40- to 80-day mussels in treatment 4 ($F_{5,1} = 9$, $P = 0.03$). The intensity of the treatment did not affect condition. Condition did not vary significantly among the four treatments for either 0- to 80- or 40- to 80-day mussels.

Accumulation of Cd by mussels

Caging mussels in Roddy Lake for 80 days did not result in a change in whole-body Cd concentrations ([Cd(body)]) compared with Lake 104 mussels freshly collected on the same day (1.62 versus 1.29 μg·g dry weight^{-1}) ($P > 0.05$). Treatment had a significant effect on Cd concentrations in 0- to 80-day mussels. Not surprisingly, treatment 1 mussels had lower [Cd(body)] than mussels in treatment 2 in the 0- to 80-day group and in treatments 2–4 in the 40- to 80-day group. This is related to lower water column Cd concentrations in treatment 1 compared with the other treatments, not only on days 0 and 40 when the mussels were introduced into the limnocorrals ($P < 0.005$) but over the entire exposure period (Fig. 2). Among treatments with the metal mixture, [Cd(body)] declined with increasing addition of the metal mixture ($F_{3,3} = 65$, $P < 0.005$) (Fig. 5*a*). As expected, the 40- to 80-day mussels, introduced into the limnocorrals on day 40, accumulated significantly less Cd than did the 0- to 80-day mussels ($P < 0.0001$). Despite the lower exposure levels, the 40- to 80-day mussels also showed the decline in [Cd(body)] with increasing addition of the metal mixture ($F_{3,3} = 57$, $P = 0.005$).

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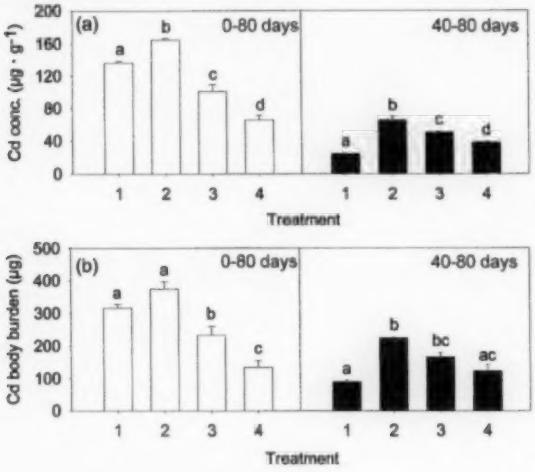
Fig. 5. Cd (*a*) concentration and (*b*) content in whole bodies (dry weight) of 0–80 and 40–80 day mussels. Bars are means ± SE for each treatment (n = 2). Bars with the same letter are not different at the P = 0.05 level (0–80 and 40–80 day mussels are statistically separate).



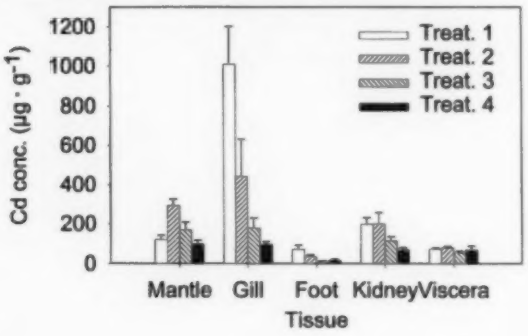
Expressing metal levels as body burdens, which adjusts for variable contribution by soft tissues to total body weight, resulted in fewer statistical differences among treatments. Nevertheless, whole-body Cd burdens among treatments showed the same trends as [Cd(body)] (Fig. 5*b*).

In general, the highest tissue Cd concentration was found in the gill followed by kidney and mantle. Like whole-body concentrations and body burdens, tissue Cd concentration declined with increasing metal mixture concentration (Fig. 6). In the gill, Cd concentrations were highest in mussels from treatment 1 and decreased with increasing concentration of the metal mixture. This trend was also observed for Cd concentrations in the foot. In the kidney, Cd levels were similar in treatments 1 and 2 and lower in treatments 3 and 4. In the mantle, Cd concentration decreased from treatment 2 to 4 with the increasing concentration of the metal mixture. There were no obvious differences among treatments in viscera Cd concentration.

Accumulation of Cu, Zn, Pb, and Ni by mussels

The 0- to 80- and 40- to 80-day mussels in the cage and in treatment 1 had background concentrations of Cu, Zn, Pb, and Ni (Fig. 7). In treatments with the metal mixture, mussels accumulated substantial amounts of Cu, Zn, Pb, and Ni (Fig. 7). Two different accumulation patterns among metals were found. Whole-body Cu, Zn, and Ni concentrations in 0- to 80- and 40- to 80-day mussels generally did not reflect the proportional increase in metals added to the limnocorrals in treatments 2–4. Lead was the only metal to reflect the increasing metal concentrations among treatments; this was observed in both the 0- to 80- and 40- to 80-day mussels (Fig. 7*c*). Whole-body Pb concentrations in treatment 4 mussels were significantly higher than in treatment 2 mussels (40- to 80-days, $F_{3,3}$ = 348, P < 0.0005; 40- to 80-days, $F_{3,3}$ = 69, P < 0.005).

Fig. 6. Cd concentration in five tissues (dry weight) of 0–80 day mussels. Bars are means ± SE for each treatment (n = 1).



Discussion

Partitioning of Cd in the water column

The presence of the metal mixture had a significant effect on the partitioning of Cd in the water, resulting in increased residence times for Cd in the water column and higher concentrations in the water at each sampling compared with the treatment without the mixture. Radioisotope studies performed at the ELA using shallow limnocorrals showed that metals are removed from the water column by two primary mechanisms: (*i*) adsorption onto particulate material and subsequent settling to the bottom of the limnocorrals and (*ii*) adsorption directly onto sediments after diffusion through a stagnant film (diffusive sublayer) overlaying the sediments (Santschi et al. 1986). In the present study, both removal processes may have been influenced by some form of competition among metals for binding sites resulting in longer residence time for Cd in the water column. For example, the lower particulate K_d^a in treatments 2–4 on day 0 suggests that there was less Cd adsorbed onto particles in the presence of other metals, thus reducing the removal of Cd from the water column by settling particles. Furthermore, the distinctly lower sediment K_d^a in treatments with the metal mixture strongly suggests that binding sites on the surface sediment (approximately the top 1 mm) may have initially been saturated by the metals, leading to increased competition and decreased adsorption. Santschi et al. (1986) found that the apparent K_d for ^{59}Fe adsorption onto suspended particles was smaller in a limnocorral that received an addition of stable Fe, resulting in a slower removal of stable Fe from the water column. The authors suggested that the increased Fe loading saturated the adsorption capacity of the particles. Despite the possibility of initial saturation of surface sediments in this experiment, it is unlikely that the sediments were completely saturated and unable to absorb more metal because by day 80, Cd concentrations in sediment were similar among treatments. Over time, metal-laden particles move deeper into sediments by physical processes and molecular diffusion opening up new binding sites at the sediment–water interface (Santschi et al. 1986). Adsorption onto limnocorral walls and colonizing organisms was not found to play a significant role in the removal of metals from the water column in the Santschi et al. (1986) experiments (<5%) and therefore was not considered in the present study. This ex-

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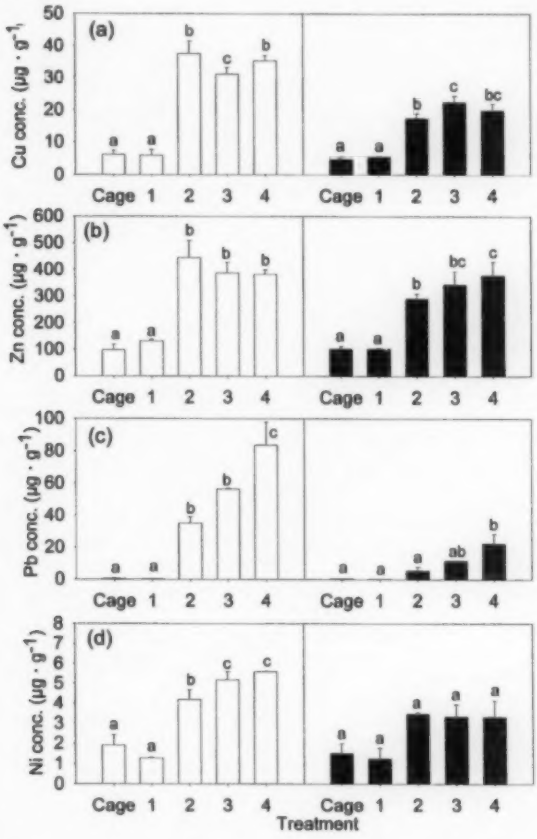
Fig. 7. Concentrations of (*a*) Cu, (*b*) Zn, (*c*) Pb, and (*d*) Ni in whole bodies (dry weight) of 0–80 day mussels (open bars) and 40–80 day mussels (solid bars). Bars are means ± SE for each treatment (n = 2). Bars with the same letter are not different at the P = 0.05 level (0–80 and 40–80 day mussels are statistically separate).



trapolation was valid, since the two experiments were similar in conception (materials, wall to sediment surface area ratio, and chemistry), and mass balance estimates in the present study for water and sediment account for all of the added Cd on day 0, prior to the addition of the mussels.

Various metals are thought to sorb predominantly to different molecular binding sites, but some sites may be mutually shared (Sigg et al. 1987). The result would be competition among metals for mutually shared sites. For example, Benjamin and Leckie (1980) found that Zn had a greater effect than Cu or Pb on Cd adsorption onto oxides, suggesting that Cd and Zn may have some shared binding sites. On a molar basis, there was five to seven times more Cu, Pb, and Ni and 43 times more Zn than Cd added to the limnocorrals in the present study. The high ratio of Zn to Cd makes it likely that Zn had the greatest impact on the sorption of Cd to particles.

Competition from Ca and Mg has also been shown to decrease Cd adsorption onto particulate matter (Laxen 1985; Cowan et al. 1991). It has been shown that Ca (2.5 mM) reduced the sorption of Cd (1 μM) to amorphous iron oxyhydroxide, due to competition for mutually accessible surface sites (Cowan et al. 1991). Furthermore, Ca concentrations as low as 0.25 mM were also found to cause the desorption of Cd from amorphous iron oxyhydroxide. Chemical analysis of the water showed relatively low Ca concentrations that increased with metal addition on days 0, 40, and 80 (0.06 mM in treatment 1 versus 0.1 mM in treatment 4 on day 80).

Differences in pH among the treatments (6.78–7.04) on day 0 were sufficient to influence the partitioning of Cd in the water column, but the result was contrary to that predicted. The higher pH in treatments 3 and 4 relative to treatments 1 and 2 on day 40 should have resulted in a higher particulate K_d^a, which was not the case (see Fig. 3). Wagemann et al. (1994) reported a significant shift of Cd from ionic Cd^{2+} to particulate-bound Cd at pH > 6.5, where the percentage of particulate Cd exceeded Cd^{2+} at around pH 7.4 (for 1.0 mg suspended sediment·L^{-1}).

The addition of the metal mixture along with Cd resulted in a decrease in the loss rate of Cd from the water column and a greater opportunity for uptake by the mussels. It is important to note that the sediments used in this study had very low background metal concentrations and that more contaminated sediments nearing saturation may have resulted in an even greater reduction in Cd removal from the water column by the metal mixture.

Factors affecting mussel condition

The condition of mussels transplanted and caged outside the limnocorrals for 80 days did not significantly differ from the condition of mussels from the source lake, suggesting that the animals did not experience significant transplant stress. This is consistent with the high degree of similarity between Roddy Lake and Lake 104 water chemistry. However, mussels held in the limnocorrals showed a loss of condition that worsened with time, suggesting stress due to the enclosure or exposure to metals. Results from acute laboratory exposures of juvenile *Anodonta imbecilis* (Keller and Zam 1991) indicate that Cu, Zn, and Cd may have been at lethal concentrations in treatment 4 at the beginning of the experiment and may have caused the observed loss in mussel condition and mortalities in this treatment. However, this observation is not supported by the fact that the loss of condition in treatment 4 mussels was only slightly greater than in mussels in treatment 1 not exposed to toxic metal mixture concentrations. The lack of a significant difference in condition among treatments in either exposure group (0–80 or 40–80 days) suggests that the length of enclosure was more important than was the treatment concentration in causing the loss of condition in the mussels. Loss of condition may be attributed to a variety of factors including metal toxicity and the abundance and nutritional quality of suspended particles filtered by the mussels. Given that the control cage (exchange with lake water) was not a true control for the enclosure effect of the limnocorral (no exchange with lake water), it is not possible to distinguish unequivocally between the effects of the enclosure and metal exposure on mussel condition.

A consequence of lower condition in mussels is artificially inflated tissue metal concentrations that can affect the conclusions drawn from a study (Salazar et al. 1996). Expressing metal accumulation on a content basis controls for losses in soft tissue weights and allows treatment groups to

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be more accurately compared. In the present study, the conclusions were essentially the same whether the metals were expressed as concentrations or as contents (Fig. 5).

Effect of the metal mixture on Cd accumulation

Despite the higher water column Cd concentrations in the presence of the metal mixture, Cd accumulation in the 0- to 80-day mussels was progressively lower with increasing concentrations of the metal mixture. This same trend was observed in 40- to 80-day mussels exposed to overall lower metal concentrations (70–90% lower, see Table 4). These results are consistent with those from other studies that examined the interactions between Cd and one or two of the metals in the mixture. Hemelraad et al. (1987) exposed the freshwater mussel *Anodonta cygnea* to Cd (25 $\mu g \cdot L^{-1}$) and to a mixture of Cd (25 $\mu g \cdot L^{-1}$) and Zn (2.5 $mg \cdot L^{-1}$) in the laboratory for 16 weeks, without food. In the presence of Zn, Cd accumulation was reduced by 50% in the whole animal and by over 50% in the gill and mantle, although it was not affected in the kidney. A similar reduction in Cd accumulation in the presence of Zn was observed in *Mytilus edulis* exposed in a laboratory factorial experiment to 20 $\mu g \ Cu \cdot L^{-1}$ and 200 $\mu g \ Zn \cdot L^{-1}$ (Elliott et al. 1986). In the present limnocorral experiment, Cd accumulation at the highest mixture concentrations in treatments 3 and 4 was lower than in treatment 1 by 26 and 50% in the whole body and by 42 and 64% in the kidney, respectively. Reduced uptake in the gill was observed at all concentrations of the metal mixture compared with treatment 1 and ranged from 56 to 91%.

A possible explanation for the reduced Cd uptake at higher concentrations of the metal mixture is that mussels spent more time with their valves closed. A reduction in the periods of valve openness and time actively filtering might be expected to reduce metal uptake. Salánki and V.-Balogh (1989) found a decrease in the duration of active filtration periods in the unionid mussel *A. cygnea* from 20 h down to 8 h and from 30–60 h down to 7 h during 240-h exposures to 10 $\mu g \ Cu \cdot L^{-1}$ and 50 $\mu g \ Pb \cdot L^{-1}$, respectively. The effect of reduced filtration activity on metal uptake in mussels is not well understood at this time. Pynnönen (1995) found that Cd concentrations in the gill of *A. cygnea* exposed in the laboratory for 2 weeks were less after exposure to 200 $\mu g \ Cd \cdot L^{-1}$ than after exposure to 50 $\mu g \ Cd \cdot L^{-1}$. Further studies identified a positive correlation between filtration activity and Cd accumulation in *A. cygnea* exposed to 50 $\mu g \ Cd \cdot L^{-1}$ (K. Pynnönen, Department of Zoology, University of Helsinki, Helsinki, Finland, personal communication). In contrast, an experiment that studied the effects of Cd, Cu, and Zn interactions on the filtration rate of the zebra mussel *Dreissena polymorpha* found that Cd was accumulated at all concentrations (10–1000 $\mu g \ Cd \cdot L^{-1}$), despite up to an 80% decrease in filtration rate (Kraak et al. 1994). Two lines of evidence in the present study suggest that reduced Cd accumulation with increasing metal mixture concentration cannot be simply explained by valve closure. It would be expected that increasing concentrations of a metal mixture would have led to progressive reduction in active filtration periods and to a reduction in food intake and consequently a loss in condition. Nevertheless, a loss of condition was not correlated with metal mixture concentration. Furthermore, reduced uptake of all the metals at higher concentrations of the mixture would have been expected and this was not observed (Fig. 6). For example, a treatment-dependent increase in Pb was observed in 0- to 80-day mussels. Relatively similar concentrations of Cu, Zn, and Ni were observed among the treatments, but concentrations of the essential metals Cu and Zn may have been determined by physiological regulation. The relationships among environmental concentrations of metals, filtering activity, and metal uptake are very important in assessing the value of mussels in bioaccumulation monitoring programs; thus, a better understanding of these relationships is needed. Specifically, studies are needed that use environmentally relevant metal concentrations and chronic exposure periods (weeks) that link thresholds for changes in filtration activity to impacts on metal uptake.

The soft tissue metal concentrations observed in this study were similar to values obtained for *P. grandis* in mining areas. Cadmium concentrations in the treated 0- to 80- and 40- to 80-day mussels ([Cd(body)] = 24–153 $\mu g \cdot g^{-1}$) were in the range of resident *P. grandis* ([Cd(body)] = 19–129 $\mu g \cdot g^{-1}$) collected along a metal contamination gradient in the Rouyn-Noranda mining region, northwestern Quebec (Couillard et al. 1993). However, Cd levels in the gill of 0- to 80-day mussels from treatments 1 and 2 (400–1000 $\mu g \ Cd \cdot g^{-1}$) were nearly four times higher than those measured in *P. grandis* collected from Rouyn-Noranda (38–270 $\mu g \ Cd \cdot g^{-1}$). The higher Cd concentrations in the gill may reflect higher water column concentrations in the present experiment compared with the exposure concentrations of the Rouyn-Noranda mussels. Furthermore, 80 days may be insufficient for metals accumulated in the gills to be translocated to other organs for storage.

Competition among metals in the environment and on biological surfaces

The aim of this experiment was to determine if metal mixtures affect the bioavailability of Cd in the aquatic environment and if the resulting available Cd concentrations influence Cd uptake in freshwater mussels. The partitioning of Cd in the water on particles and in the sediment over the course of the experiment showed that the metal mixture slowed the removal of Cd from the water column, possibly through competition for sites on settling particles and on the surface sediment. This resulted in more Cd in the water column available for uptake by the mussels in the presence of the mixture. Nevertheless, the higher water column Cd concentrations did not result in increased accumulation of Cd by freshwater mussels. It appeared that some mechanism related to the mussel and not to the distribution of Cd in the environment influenced Cd uptake.

Assuming that valve closure was not a determining factor, there are two possible explanations for these results, depending on the primary pathway of Cd uptake in freshwater mussels. If the mussels accumulate most of their metal burden from the water, then direct competition among metals for sites on the mussels (i.e., gill epithelia) might have reduced Cd uptake. Recent studies by Wang et al. (1996) using the marine mussel *M. edulis* suggest that although Cd is accumulated from both dissolved and particulate pathways, the largest portion of Cd is obtained from dissolved sources (>50–80%). The principal mechanism of Cd uptake by freshwater organisms is through binding to membrane trans-

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port ligands or by incorporation of Cd into an active pump for a major ion that deposits the metals into the interior of the cell (Rainbow and Dallinger 1993). Competition among metals may have occurred at these transport sites. A less likely alternative is that the portion of Cd accumulated from particles or "food" could have been reduced at the highest concentration of the metal mixture due to reduced sorption on particles. The lower particulate K_d^a in the treatments with the mixture on day 0 seems to suggest this, although sample variability on day 40 makes it difficult to confirm the relationship.

Current knowledge of the behavior of trace metals under varying degrees of chemical equilibrium is insufficient to allow for the broad generalization of these results. For this reason, further testing of metal mixtures at chemical equilibrium is needed. Under nonequilibrium conditions, the uncoupling of the effects of the metal mixture on Cd bioavailability and uptake suggests that laboratory studies may be appropriate for characterizing metal uptake in mussels exposed to mixtures of metals. The effect of the metal mixture to prolong the high water column Cd concentrations and reduce uptake in the mussels is a significant deviation from the behavior of Cd added alone. These results emphasize the need to further examine the appropriateness of water and sediment quality criteria developed for individual contaminants (Canadian Council of Resource and Environment Ministers 1987; Jaagumagi 1992).

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Interactions between individual feeding behaviour, growth, and swimming performance in juvenile rainbow trout (*Oncorhynchus mykiss*) fed different rations

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Abstract: Aerobic swimming performance (critical swimming speed, U_{crit}), food consumption per meal (by X-ray radiography), specific growth rate (SGR), haematocrit, and fin condition were monitored in individual juvenile rainbow trout (*Oncorhynchus mykiss*). The fish were held in groups over a 9-week period and fed daily group rations (dry food) of 2.0, 1.5, 1.0, and 0.5% wet body mass (BM)·day^{-1}. SGR declined and competition increased at lower ration levels, as reflected by greater fin damage, reduced haematocrits and condition factors, and, at 0.5% BM·day^{-1}, a substantial increase in the coefficient of variation among individual meals. Absolute U_{crit} also declined at lower ration levels. However, there was no relationship between U_{crit} and haematocrit, fin damage, or condition factor in any of the ration groups. A negative correlation was found between U_{crit} and SGR in individual trout fed a group ration of 2.0% BM·day^{-1}, but a positive correlation was seen at 0.5% BM·day^{-1} and no relationship at 1.0 and 1.5% BM·day^{-1}. There was a positive relationship between individual SGR and food consumption only among fish fed a ration of 2.0% BM·day^{-1}. A significant negative relationship between U_{crit} and individual food consumption was also found among fish in this ration group.

Résumé : On a surveillé la performance natatoire aérobie (vitesse de nage critique, U_{crit}), la consommation de nourriture par repas (par radiographie aux rayons X), le taux de croissance spécifique, l'hématocrite et l'état des nageoires chez des truites arc-en-ciel (*Oncorhynchus mykiss*) juvéniles. Les poissons étaient gardés en groupes durant 9 semaines et on les nourrissait avec des rations de groupe quotidiennes (nourriture sèche) de 2,0, 1,5, 1,0 et 0,5% de la masse corporelle fraîche (MC)·jour^{-1}. Le taux de croissance spécifique a diminué et la compétition s'est accrue aux plus faibles rations, comme en ont témoigné les dommages accrus aux nageoires, la réduction des hématocrites et des coefficients de condition et, à la ration de 0,5% MC·jour^{-1}, l'accroissement substantiel du coefficient de variation entre les repas des individus. L'U_{crit} absolue a aussi diminué aux rations inférieures. Cependant, on n'a pas observé de relation entre l'U_{crit} et l'hématocrite, les dommages aux nageoires ou le coefficient de condition dans l'ensemble des groupes, quelle que soit la ration. On a observé entre l'U_{crit} et le taux de croissance spécifique une corrélation négative chez les truites ayant reçu une ration de groupe de 2,0% MC·jour^{-1}, une corrélation positive chez les truites ayant reçu une ration de 0,5% MC·jour^{-1} et aucune relation chez celles ayant reçu une ration de 1,0 et de 1,5% MC·jour^{-1}. Il y avait une relation positive entre les taux de croissance spécifiques individuels et la consommation de nourriture seulement chez les poissons ayant reçu une ration de 2,0% MC·jour^{-1}. Enfin, dans ce même groupe de poissons, on a observé une relation négative significative ente l'U_{crit} et la consommation individuelle de nourriture.

[Traduit par la Rédaction]

Introduction

It is becoming increasingly clear that in fish, there exist complex relationships among feeding, growth, and other key elements of fitness such as swimming performance. For example, trade-offs between growth rate and aerobic swimming capacity have now been reported in several fish species (Kolok and Oris 1995; Farrell et al. 1997; Gregory and Wood 1998). Thus, under certain conditions, individual fish may be able to maximize either growth rate or swimming performance, but not both. This trade-off is potentially puzzling, since the activities of key muscle enzymes are known to correlate positively with aerobic swimming performance (Farrell et al. 1991; Kolok 1992*b*) and growth rate (Goolish and Adelman 1987).

Several possible explanations exist, including differences in body size (Beamish 1978), morphology (Taylor and McPhail 1985), and haematocrit (Gregory and Wood 1998) associated with growth. It has also been suggested that energetic costs associated with the digestion and conversion of food could have deleterious effects on aerobic swimming performance (Alsop and Wood 1997; Gregory and Wood 1998), but to date, the effect of feeding level on swimming performance has not been examined directly. The results of a previous study using juvenile rainbow trout (*Oncorhynchus*

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Table 1. Mean values ± SE (n) of the various parameters measured for fish in the 2.0, 1.5, 1.0, and 0.5% BM·day^{-1} ration groups.

Variable	2.0% BM·day^{-1}	1.5% BM·day^{-1}	1.0% BM·day^{-1}	0.5% BM·day^{-1}
Initial mass (g)	5.54±0.18 (25) *a*	5.57±0.16 (25) *a*	5.40±0.17 (25) *a*	5.52±0.18 (25) *a*
Food consumption (%BM·day^{-1})	2.05±0.10 (25) *a*	1.57±0.06 (23) *b*	1.11±0.04 (23) *c*	0.56±0.06 (22) *d*
Overall SGR (%·day^{-1})	1.79±0.07 (25) *a*	1.43±0.07 (23) *b*	0.81±0.06 (23) *c*	0.11±0.03 (22) *d*
Condition factor (100 × g × cm^{-3})	1.29±0.02 (25) *a*	1.24±0.02 (23) *a*	1.16±0.01 (23) *b*	1.06±0.02 (22) *c*
Haematocrit (% volume)	45.70±0.88 (20) *a*	46.84±0.73 (19) *a*	42.20±0.90 (20) *b*	38.52±0.93 (21) *c*
CV (%)	31.52±2.43 (25) *a*	28.83±2.64 (23) *a*	34.65±2.69 (23) *a*	59.75±4.39 (22) *b*
Fin score	35.56±0.51 (25) *a*	33.83±0.58 (23) *ab*	31.61±0.83 (23) *b*	26.83±0.90 (22) *c*
Swim length (cm)	10.50±0.16 (24) *a*	9.77±0.16 (22) *b*	9.07±0.18 (18) *c*	8.27±0.09 (20) *d*
Swim SGR (%·day^{-1})	2.20±0.11 (24) *a*	1.70±0.08 (22) *b*	1.02±0.10 (18) *c*	0.15±0.11 (20) *d*
Relative U_{crit} (BL·s^{-1})	4.23±0.14 (24) *a*	3.82±0.11 (22) *ab*	4.16±0.19 (18) *a*	3.42±0.10 (20) *b*
Absolute U_{crit} (cm·s^{-1})	44.21±1.26 (24) *a*	37.35±1.32 (22) *b*	37.72±1.86 (18) *b*	28.37±1.08 (20) *c*

Note: Differences in sample size reflect mortality or problems with blood sampling in small fish. In addition, fish that refused to swim or escaped from the swim tunnels were omitted from the data set. Different letters represent significant differences ($p < 0.05$).

mykiss) suggested that the trade-off occurred only below a certain ration level (Gregory and Wood 1998), but the precise range of food intakes over which this relationship occurs was not investigated in detail. As such, the primary goal of the present study was to evaluate the roles of body size, morphology, haematocrit, and feeding in the development of this trade-off and to determine the range of rations over which it occurs. By beginning at the level where trade-offs were seen previously (~2% body mass (BM)·day^{-1}, Gregory and Wood 1998) and decreasing to roughly one quarter of this amount (to ~0.5% BM·day^{-1}), and by measuring the feeding behaviours, growth characteristics, and swimming performances of the same individual trout, many questions raised by the results of previous studies can be addressed directly.

Before any relationships involving swimming performance can be considered biologically relevant, the repeatability of individual swimming ability must be demonstrated. Individual swimming performance has been found to be significantly repeatable among largemouth bass (*Micropterus salmoides*) (Kolok 1992*a*) and among juvenile rainbow trout swum in small groups (Gregory and Wood 1998), but the repeatability of swim performance among trout swum individually remains to be shown. In addition, it is desirable to determine whether the trade-off between aerobic swimming performance and growth rate reported previously (Gregory and Wood 1998) was simply an artefact of the social interactions present among fish swimming in groups. The resolution of these issues represents the second goal of the present study.

In addition to the processes associated with the ingestion and assimilation of food, social interactions may play an important role in determining the growth rates of individual fish. Recent studies employing X-ray radiography have shown that feeding rank can have a significant impact on the amount of food obtained by individuals and therefore affect growth (McCarthy et al. 1992; Gregory and Wood 1998). Moreover, as ration decreases and competition for food increases, there may be further impacts on growth resulting from heightened levels of stress and energetic expenditure as aggressive interactions become intensified (Moutou et al. 1998). In this regard, the third goal of the present study was to examine the effects of group ration on the strength of the feeding hierarchy formed and the possible consequences of aggressive interactions between individual fish.

Materials and methods

Experimental animals and design

Juvenile rainbow trout (4–8 g) were obtained from Humber Springs Trout Hatchery in Orangeville, Ontario. The fish were kept at 15 ± 1°C in dechlorinated Hamilton, Ontario, tapwater (composition reported in Alsop and Wood 1997) with a photoperiod of 12.5 h light : 11.5 h dark. Fish were screened for healthy dorsal and caudal fins, weighed to the nearest 0.01 g, measured for fork length to the nearest 0.1 cm, and marked for identification using a PanJet ink injector and Alcian Blue dye. The fish were re-marked again every 4 weeks to ensure accurate identification of individuals. Twenty-five fish were placed in each of four square 60-L tanks (flow-through rate ~1.0 L·min^{-1}), with no significant differences in mean initial mass among tanks ($p > 0.91$) (Table 1). The fish in the four tanks were fed once per day (between 10:00 and 11:00) on one of four rations, 2.0, 1.5, 1.0, or 0.5% BM·day^{-1}, using commercial trout food (Ziegler Bros., Inc., Gardners, Pa.) that was powdered in a standard kitchen blender, mixed with water, and then repelleted using a pasta maker.

The fish were allowed to grow for 3 weeks and were weighed and measured weekly (without anaesthesia). After this initial growing period, swim trials were initiated, a process that lasted a further 6 weeks. During this period, weekly measurements of mass and length were continued, together with repetitive X-ray analyses of individual food consumption (see below). No fish were swum on the day immediately following X-raying.

Swimming performance

On swimming days, a single fish was selected from each tank and placed into one of four 3.23-L Blazka-type swimming respirometers. The respirometers were calibrated prior to use with a Kent Microflo type 265 propellor-style flowmeter and kept in a temperature-controlled water bath at 16 ± 1°C. Individuals were allowed to habituate to the swim tunnels at 1 body length (BL)·s^{-1} for at least 2.5 h and were fasted for a minimum of 27 h prior to swimming. The velocity of the water was increased by 0.75 BL·s^{-1} every 40 min until the fish could no longer be prompted to swim by temporarily lowering or raising the velocity or by gently shaking the tunnel, at which time the fish was judged exhausted. A shocking grid was not employed, in accord with animal care regulations. Each fish was weighed and measured after exhaustion and then returned to its holding tank until the end of the 9-week period (with the exception of weekly weighing and X-raying). Relative critical

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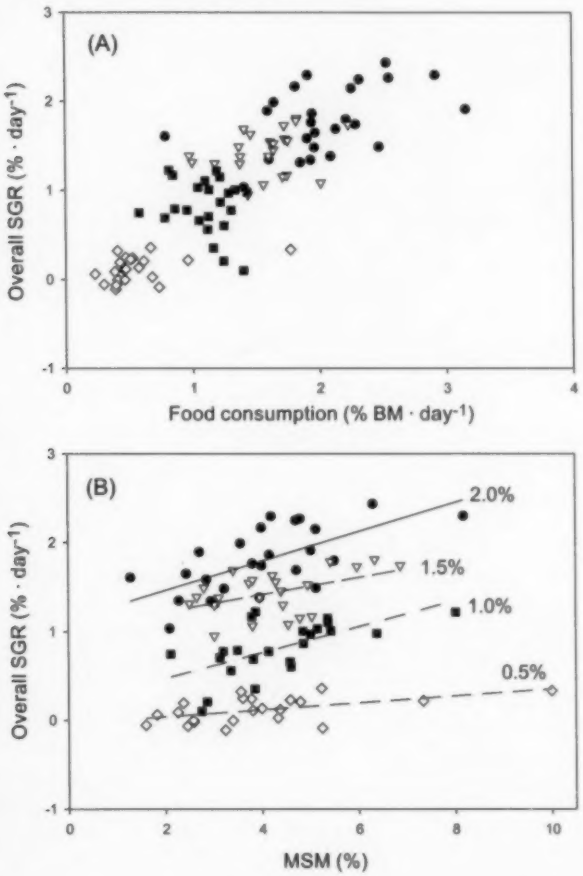
Fig. 1. Relationships between individual (A) mean daily food consumption and (B) MSM and overall SGR and for fish in the 2.0% (●), 1.5% (▽), 1.0% (■), and 0.5% (◇) BM·day^{-1} ration groups. In Fig. 1A, there was a significant positive regression between food consumption and overall SGR among fish in the 2.0% BM·day^{-1} group ($r^2 = 0.2896$, $p < 0.03$) and when the data were pooled ($r^2 = 0.7022$, $p < 0.0001$) but not within any of the other ration groups (all $p > 0.11$). Regressions in Fig. 1B were as follows: 2.0%, $r^2 = 0.4261$, $p < 0.001$, $n = 25$, $y = 0.17x + 1.13$; 1.5%, $r^2 = 0.2182$, $p < 0.03$, $n = 23$, $y = 0.10x + 1.03$; 1.0%, $r^2 = 0.3859$, $p < 0.002$, $n = 23$, $y = 0.15x + 0.18$; 0.5%, $r^2 = 0.2141$, $p < 0.04$, $n = 22$, $y = 0.03x + 0.02$. There were no significant differences in slopes among these regressions ($p > 0.30$), although the elevations of the lines were significantly different from one another (all $p < 0.001$).



swimming speed (U_{crit}, body lengths per second) and absolute U_{crit} (centimetres per second) were calculated for each fish as in Brett (1964). Each fish was swum only once.

The specific growth rate (SGR, percent per day) of each fish was calculated as in Kolok and Oris (1995) over two different time periods: "overall SGR" (initial mass to final mass, a period of roughly 9 weeks) and "swim SGR" (initial mass to mass at time of swimming, the same as "SGR" used in Gregory and Wood (1998)). Condition factor (100 × mass × length^{-3}) and maximum cross-sectional area (π [(0.5 × maximum height)(0.5 × maximum width)], Kolok and Oris 1995) were also calculated for each fish at the time of swimming. In addition, a group of eight fish (10–25 g) was tested for repeatability of swimming performance exactly as described in Gregory and Wood (1998), except that the fish were swum individually in one of the 3.23-L Blazka-type respirometers rather than communally in a single 100-L Beamish-type respirometer.

X-ray radiography

In order to evaluate the feeding patterns of individuals, the fish were X-rayed on four separate occasions beginning at the start of week 6, with 1 week recovery periods during which the feeding regime was maintained (see McCarthy et al. 1992, 1993; Gregory and Wood 1998). On these days, the fish were fed food that was repelleted in the same manner as the regular diet but that contained 8.5-grade (0.400- to 0.455-mm) lead glass ballotini beads at fixed density (6% by dry mass of food) (Jencons USA, Inc., Bridgeville, Pa.). The ballotini beads did not affect the palatability of the food, which was completely consumed as in regular feeding. In order to prevent regurgitation caused by anaesthesia, the fish were allowed to settle for at least 1 h prior to X-raying. After this time, groups of 10 fish were identified and placed into a 10-part glass grid filled with water, which was then drained and filled with 0.1 g tricaine methanesulfonate (MS 222)·L^{-1} and set to a pH of ~8.0 with 3 M NaOH. X-raying was carried out using a General Electric AMX-110 mobile X-ray machine with a 70 kVP (kilovolts peak), 150 mAs (milliampere seconds) exposure at 61 cm. The fish were returned to the holding tanks immediately following X-ray exposure and the process repeated until all fish had been X-rayed. The X-ray films were then developed and the number of beads located in the digestive tract counted for each fish. No regurgitation or clearance of beads was observed, and all X-raying was completed within 2 h of feeding. The total number of beads found within all of the fish in a tank was used to calculate the mean share of meal (MSM) obtained by each individual fish (McCarthy et al. 1992). In addition, coefficient of variation (CV, a measure of the day-to-day variability in food consumption of each individual fish) was calculated as in McCarthy et al. (1992).

The conditions of the dorsal and caudal fins were evaluated prior to the commencement of swimming trials at the start of week 4 and again at each X-ray period (weeks 6–9) and assigned a numerical value between 1 (poor) and 4 (excellent) according to the absolute amount of damage present. These values were then added together to give a final "fin score" that served as an indication of the total amount of damage sustained by each individual during the experimental period (i.e., maximum possible score = 40) (Gregory and Wood 1998). An index of fin condition was also tabulated for each ration group using the equation given in Moutou et al. (1998) and used to assess the relationship between fin condition and ration at various times throughout the experiment.

After the completion of the X-raying and swim trials, the fish were sacrificed individually in 1.0 g MS 222·L^{-1}, weighed, and measured and a blood sample taken by caudal severance. Haematocrits were measured following 5 min of centrifugation at 5000 *g*.

Statistical analysis

Statistical analyses were performed using Statistix v1.0 for Windows (© 1996 Analytical Software), SigmaPlot v4.0 for Windows 95 (© 1997 SPSS, Inc.), and Quattro Pro v7.0 for Windows 95 (© 1996 Corel Corporation Ltd.). Correlations and regressions consisted of Pearson correlation analyses and least-squares regression, and comparisons of regression slopes and elevations were carried out using ANCOVA and the Tukey test of multiple comparison (Zar 1996). The repeatability of swim performance was assessed using Spearman rank correlation analysis. Differences in group

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means were evaluated using two-sample t tests or one-way ANOVA followed by Tukey tests. All averages are reported as mean ± SE (n).

Results

Growth

The mean individual food consumptions in the four tanks, based on four separate X-ray analyses over the 9-week experiment, corresponded almost exactly to the group rations of 2.0, 1.5, 1.0, and 0.5% BM·day^{-1} (Table 1). There were significant differences in mean overall SGR (i.e., over the entire experimental period) among these tanks, with the 0.5% ration group showing a mean SGR somewhat lower than would be predicted based on ration alone (Table 1). Not surprisingly, when the data from all four groups were considered together, there was a strong positive correlation between overall SGR and individual food consumption (r = 0.838, $p < 0.0001$) (Fig. 1). Overall SGR showed a positive correlation with individual food consumption only among fish fed a 2.0% BM·day^{-1} ration ($r = 0.538$, $p < 0.03$; others, $p > 0.11$).

Fish in the 0.5% BM·day^{-1} group showed significantly lower condition factors than those in the 1.0% BM·day^{-1} group. There were no significant differences in condition factor between fish in the 2.0 and 1.5% BM·day^{-1} tanks, but these fish had significantly higher condition factors than fish in the other two tanks (Table 1). In all tanks, condition factor was unrelated to both food consumption (all $p > 0.05$) and SGR (all $p > 0.28$). Haematocrit followed qualitatively similar relationships as those for condition factor (Table 1). In addition, haematocrit was unrelated to both individual food consumption (all $p > 0.05$) and overall SGR (all $p > 0.11$) in all ration groups. Significant correlations between haematocrit and fin score were found only in the 1.5% ($r = -0.644$, $p < 0.004$) and 1.0% BM·day^{-1} groups ($r = 0.691$, $p < 0.009$; note the difference in sign between these groups; others, $p > 0.15$), indicating that haematocrits were not affected by blood loss associated with fin damage.

Feeding rank

Fish in the 0.5% BM·day^{-1} group showed a significantly higher mean CV than fish in all other tanks ($p < 0.0001$), indicating higher variability among the four separate meals recorded by X-ray radiography for each fish. There were no differences in mean CV among any of the other diet groups, however (Table 1). CV was not significantly correlated with overall SGR (all $p > 0.32$) or MSM in any of the tanks, although overall SGR was positively correlated with MSM in all tanks (all $r \geq 0.463$, all $p < 0.03$) (Fig. 1B). The slopes of the regression lines were not significantly different from one another, but there were significant differences in the elevations of the regression lines between all diet groups (all $p < 0.001$).

In general, fish fed lower rations showed higher levels of fin damage, as reflected by significantly lower mean fin scores (Table 1). Individual fin score was positively correlated with MSM in the 1.0% BM·day^{-1} group ($r = 0.571$, $p < 0.005$) and showed a similar but nonsignificant trend in the 0.5% BM·day^{-1} group ($r = 0.378$, $p < 0.076$), but was unrelated to both MSM and CV in all other cases (all $p > 0.11$). Similarly, individual fin score showed positive relationships with initial mass in the 1.0% ($r = 0.515$, $p < 0.012$) and 0.5% BM·day^{-1} ration groups ($r = 0.546$, $p < 0.007$), suggesting that smaller fish received more fin damage in these low-ration tanks. There were no such relationships in the two higher ration tanks (all $p > 0.31$). Fin condition indices (as calculated in Moutou et al. 1998) for the caudal fin and total fin measurements were positively correlated with ration at weeks 7, 8, and 9 (all $r > 0.94$, all $p < 0.05$) but not for the first two measurement periods (weeks 4 and 6). Dorsal fin condition index was not significantly correlated with ration at any of the measurement periods (all $p > 0.06$) but followed a qualitatively similar pattern as that for the caudal and total fin condition indices (Fig. 2). Dorsal fins typically received more damage than caudal fins, as reflected by their lower fin condition indices (Figs. 2A and 2B).

Swimming performance

Individual swimming performance was significantly repeatable when the fish were swum individually (Spearman rank correlation coefficient, one-tailed, $\rho = 0.735$, $p < 0.05$) and very comparable with earlier results where fish were swum communally in a much larger swim tunnel (Gregory and Wood 1998). There were no significant differences in mean relative U_{crit} between the two trials ($p > 0.52$), indicating no improvement or reduction in performance from one trial to the next.

Fish in the 0.5% BM·day^{-1} group showed the poorest aerobic swimming performance, both in terms of relative U_{crit} (body lengths per second) and absolute U_{crit} (centimetres per second) (Table 1). The relative U_{crit} values of fish in the 2.0% BM·day^{-1} group were not significantly different from those in the 1.5 and 1.0% BM·day^{-1} groups (Table 1), but these fish showed a significantly higher mean absolute U_{crit} than fish in the other tanks, reflecting their greater length (Table 1).

There was a significant negative correlation between relative U_{crit} and swim SGR among fish in the 2.0% BM·day^{-1} tank ($r = -0.477$, $p < 0.02$) (Fig. 3A). A similar relationship was found between absolute U_{crit} and swim SGR in this group ($r = -0.446$, $p < 0.03$) (Fig. 3B). Significant positive correlations were found between both relative ($r = 0.576$, $p < 0.008$) and absolute U_{crit} ($r = 0.610$, $p < 0.005$) and swim SGR in the 0.5% BM·day^{-1} fish (Fig. 3). No such relationships were found in either the 1.5 or 1.0% BM·day^{-1} group (all $p > 0.26$).

In the 2.0% BM·day^{-1} group, there was a negative relationship between U_{crit} and food consumption ($r = -0.460$, $p < 0.03$) (Fig. 4). There were no significant relationships between U_{crit} and food consumption in the other ration groups (all $p > 0.12$). Similarly, there was a negative relationship between U_{crit} and MSM in the 2.0% BM·day^{-1} group ($r = -0.658$, $p < 0.001$) but not among any of the other groups (all $p > 0.09$). None of the tanks showed a relationship between either relative (all $p > 0.27$) or absolute U_{crit} (all $p > 0.07$) and number of growing days prior to swimming, indicating that differences in swimming performance between individuals were not greatly affected by the swimming schedule used.

The possibility of spurious relationships among U_{crit}, SGR, and body size was also investigated. Both relative and absolute U_{crit} showed significant positive correlations with indi-

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Fig. 2. (A) Caudal fin condition index, (B) dorsal fin condition index, and (C) total fin condition index calculated at weeks 4, 6, 7, 8, and 9 for fish in the 2.0% (●), 1.5% (▽), 1.0% (■), and 0.5% (◇) BM·day^{-1} ration groups. Higher condition index values indicate less fin damage. All fish were screened for a minimum level of fin quality prior to placement in the holding tanks such that all fish began the experiment with similar fin conditions. Relationships between ration and fin condition are discussed in the text. Note the axis break in Fig. 2A.

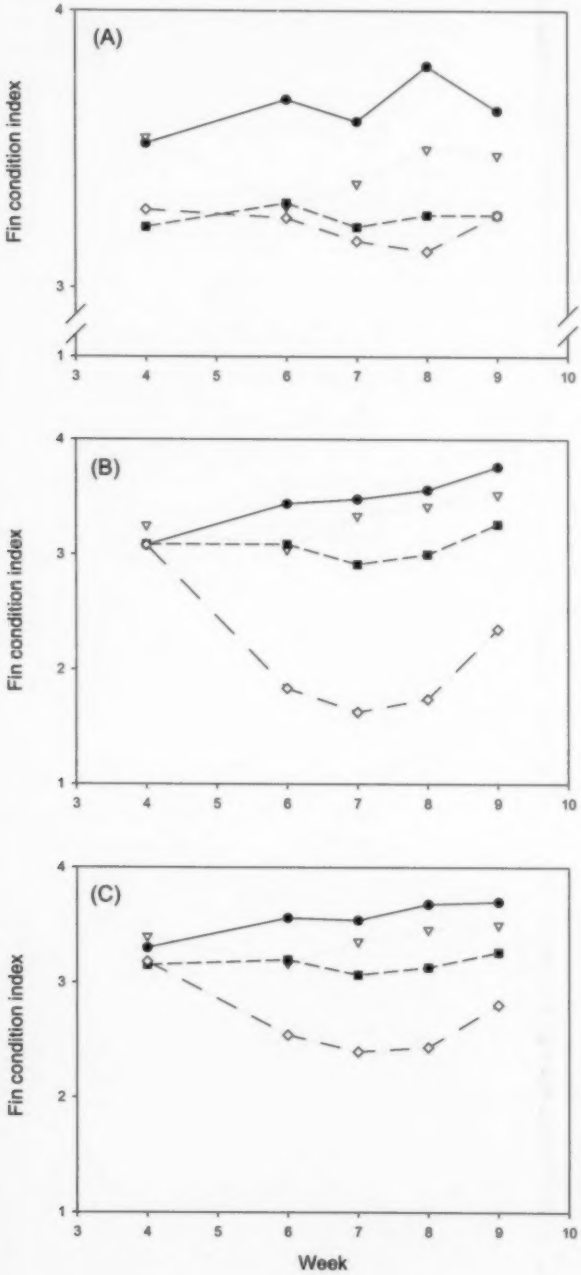
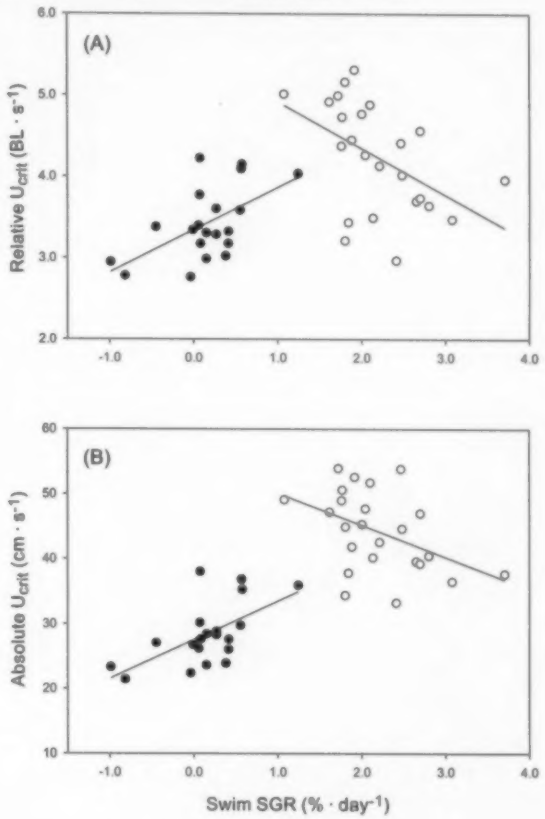


Fig. 3. Relationship between (A) relative U_{crit} and swim SGR and (B) absolute U_{crit} and swim SGR among fish fed on 2.0% (○) and 0.5% (●) BM·day^{-1} rations. Significant *negative* regressions were found between relative U_{crit} and SGR (r^2 = 0.2300, $p < 0.02$, $n = 24$, $y = -0.57x + 5.49$) and absolute U_{crit} and SGR (r^2 = 0.1987, $p < 0.03$, $n = 24$, $y = -4.93x + 55.03$) in the 2.0% BM·day^{-1} group. Significant *positive* regressions were found between relative U_{crit} and SGR (r^2 = 0.3319, $p < 0.008$, $n = 20$, $y = 0.52x + 3.34$) and between absolute U_{crit} and SGR (r^2 = 0.3716, $p < 0.005$, $n = 20$, $y = 5.98x + 27.48$) in the 0.5% BM·day^{-1} group. No such relationships were found in the 1.5 and 1.0% BM·day^{-1} ration groups (all $p > 0.26$).



cators of body size (mass, length, and cross-sectional area) in the 0.5% BM·day^{-1} group (all $r \geq 0.536$, all $p < 0.02$). These relationships were absent in the 1.0% BM·day^{-1} group (all $p > 0.08$). In the 1.5% BM·day^{-1} group, there were significant positive correlations between body size and absolute U_{crit} only (all $r \geq 0.471$, all $p < 0.03$), while in the 2.0% BM·day^{-1} group, there were significant negative correlations between body size and relative U_{crit} only (all $r \leq -0.491$, all $p < 0.02$). More importantly, swim SGR was found to be unrelated to indicators of body size in both the 2.0 and 1.5% BM·day^{-1} groups (all $p > 0.08$) but was significantly positively correlated with body size in the 1.0 and 0.5% BM·day^{-1} groups (all $r \geq 0.459$, all $p < 0.03$). Neither relative nor absolute U_{crit} was significantly correlated with haematocrit, condition factor, or fin score in any of the tanks (all $p > 0.05$).

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Discussion

Growth

Since the energy required for growth is obtained in the diet, food intake necessarily affects the growth rates of fish. However, at lower rations, where there is intensified competition for food and a more strictly enforced hierarchy (McCarthy et al. 1993), there is a disproportionate decrease in mean growth rate (Table 1). This depression of growth at low rations is most likely the result of increased energy expenditure and stress levels as individuals compete for food (Metcalfe 1986; Abbott and Dill 1989).

It is important to note that the positive relationship between overall SGR and food consumption was significant only among fish fed a 2.0% BM·day^{-1} ration but not when rations were higher (Gregory and Wood 1998) or lower (present study). At high rations, the costs associated with the digestion and conversion of food (i.e., specific dynamic action, Alsop and Wood 1997), the reduction of growth efficiency as fish become larger (Wurtsbaugh and Davis 1977), and the increase in gastric evacuation rate (and associated decrease in absorptive efficiency) that occurs with increasing ration (Wurtsbaugh and Davis 1977; Jobling 1994) may contribute to a system of "diminishing returns" whereby beyond a certain maximum food intake, there is no further benefit to growth rate as ration increases (Fig. 1; also see Gregory and Wood 1998). At very low rations, the relationship between food intake and SGR is presumably not significant, simply because there is little difference in the actual food consumptions of individual fish. This lack of separation of the data therefore makes the resolution of any relationships very difficult. In the case of MSM, where there was a more profound separation of the data, significant positive relationships between SGR and MSM were found under all rations (Fig. 1B).

Fish in the low-ration tanks also showed lower condition factors and haematocrits (Table 1). The first of these suggests a higher level of protein and lipid catabolism among these fish (Barton et al. 1987). Although morphological differences may influence the relative swimming performances of fish from fast- versus slow-growing strains (Taylor and McPhail 1985), the lack of association between morphological characteristics (i.e., condition factor, a measure of the "bulkiness" of a fish) and either growth rate or swimming performance in the present study suggests that changes in body shape of this type are not responsible for the relationships between SGR and U_{crit} observed among individual fish.

Differences in haematocrit probably did not result from blood loss associated with higher levels of fin damage (see below) in the fish, since there was no correlation between haematocrit and fin score. Instead, the lower haematocrits probably resulted from the insufficient energy and nutrient intake among these fish, limiting their ability to produce somatic tissues of various types (including red blood cells). More importantly, haematocrit was found to be unrelated to both growth rate and swimming performance in the present study. Experimental manipulations of haematocrit over a larger range have been shown to affect swimming performance, with increased haematocrit resulting in increased performance (Gallaugher et al. 1995). However, this relationship may be of limited biological significance and certainly does not explain the SGR versus swimming performance trade-off, thereby discounting the earlier suggestion of Gregory and Wood (1998).

Feeding rank

In accordance with previous studies using one daily feeding (McCarthy et al. 1992), and in contrast with a previous study that employed three daily meals (Gregory and Wood 1998), fish fed on the lowest ration in the present study showed a significantly higher mean CV than the fish in all other ration groups (Table 1). This result indicates more variable individual feeding patterns from day to day in a situation where competition for food is intensified. However, CV was not related to any other potential indicators of social rank, such as MSM, fin score, or individual food consumption. In addition, CV has been shown to be altered significantly by elevations in plasma cortisol levels independent of social interactions (Gregory and Wood 1999). Although CV has previously been found to correlate with MSM (McCarthy et al. 1992), which in turn has been correlated with indicators of social rank such as brain serotonin activity (Winberg et al. 1993), the results of the present study suggest that CV may not always provide a reliable index of feeding rank in fish (cf. McCarthy et al. 1992, 1993; Winberg et al. 1993; Jobling 1994).

The dorsal and caudal fins are the primary sites of aggressive attack among juvenile rainbow trout (Abbott and Dill 1985), with the dorsal fin typically receiving more damage than the caudal fin (Abbott and Dill 1985, 1989; Moutou et al. 1998; present study). Under low-ration conditions (1.0 and 0.5% BM·day^{-1}), MSM and initial mass were positively related to fin score, suggesting that there were higher levels of aggression in these tanks as a result of more intense competition for food or the enforcement of a more strict dominance hierarchy (Davis and Olla 1987; Olla et al. 1992; Moutou et al. 1998). In addition, caudal and total fin condition indices were positively correlated with ration level at weeks 7, 8, and 9 (but not at the earlier measurements), suggesting that there were higher levels of aggressive attacks in the low-ration tanks whose effects became apparent after a few weeks. It is also possible that the intensified competition for food leads to higher stress levels among low-ration fish, resulting in decreased fin conditions arising in part from the reduced immunity and tissue repair associated with plasma cortisol elevation (Pickering and Pottinger 1989; Gregory and Wood 1999).

Swimming performance

The swimming performances of rainbow trout swum individually were repeatable in this study, similar to the repeatability when fish are swum communally in small groups (Gregory and Wood 1998). This result suggests that either swimming fish in groups or swimming them individually is an acceptable approach for studies of this sort. This consistency further supports the view expressed by several researchers (Bennett 1987; Kolok 1992*a*; Gregory and Wood 1998, 1999) that variation among individuals should be seen as a valuable experimental resource rather than a statistical annoyance.

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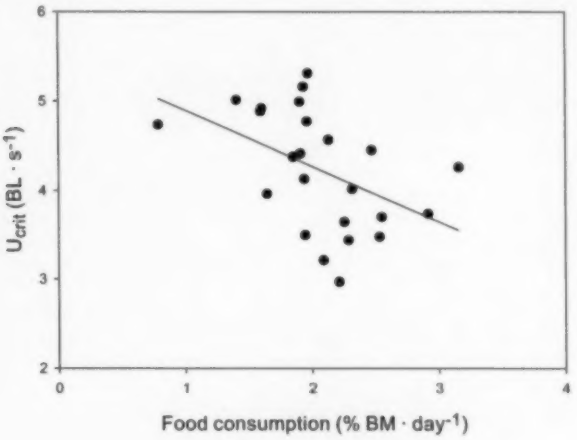
Fig. 4. Relationship between relative U_{crit} and individual food consumption for fish in the 2.0% BM·day^{-1} ration group (r^2 = 0.2111, $p < 0.03$, $n = 24$, $y = -0.62x + 5.52$). No such relationships were found in any of the other ration groups (all $p > 0.12$).



More importantly, the negative relationships between SGR and relative U_{crit} reported in Gregory and Wood (1998) have been confirmed and occurred over a similar range of food intakes as in that study (Fig. 3A). Thus, even when the possibility of social interactions is removed by swimming the fish individually rather than communally, the relationships persist. In addition, there was a negative relationship between SGR and absolute U_{crit} among fish in the appropriate ration group (Fig. 3B), which confirms the results reported by Kolok and Oris (1995) using fathead minnows (*Pimephales promelas*).

The results of the present study have also clarified the issue of possible spurious correlations between SGR and U_{crit} resulting from the well-established relationships between U_{crit} and body size. In the present study, both swim SGR and indicators of body size were negatively correlated with U_{crit}, but because the swimming schedule used resulted in differences in the lengths of growth periods for individual fish, there were no correlations between body size and swim SGR in the relevant ration group. Thus, growth rate itself, independent of effects on body size, significantly affects the swimming performance of individual fish. This is consistent with the findings of Farrell et al. (1997) who found that growth-enhanced transgenic salmon showed a reduction in swimming performance that could not be explained on the basis of differences in body size alone.

This negative relationship between swim SGR and U_{crit} is seen only among fish fed a 2.0% BM·day^{-1} ration and is not apparent at higher rations (~4% BM·day^{-1}, which represents satiation, Gregory and Wood 1998) or lower rations (≤1.5% BM·day^{-1}). Moreover, the significant negative relationship between U_{crit} and individual food consumption (Fig. 4) clearly indicates that the costs associated with feeding, digestion, and conversion of food to somatic tissue are largely responsible for the emergence of this trade-off. At a very low ration (0.5% BM·day^{-1}), on the other hand, the relationship reverses sign and becomes positive, with higher growth rates resulting in heightened swimming performance. It is therefore apparent that below a certain threshold, there is insufficient energetic intake to invest in either growth or swimming performance and that under conditions of very low rations, only those fish that receive a certain amount of food are able to both grow and swim effectively. Thus, the observed trade-off between SGR and U_{crit} may occur only over a range of food intakes from roughly 2.0 to 4.0% BM·day^{-1}, disappearing above and below this level and switching to a positive relationship below a certain threshold around 0.5% BM·day^{-1} where many fish exhibit negative growth rates.

Our findings are of potential importance in programs of captive breeding and reintroduction into the wild, since the range (i.e., 2.0–4.0% BM·day^{-1}) for which the potential trade-off occurs precisely is that recommended in aquaculture for the size of fish and water temperatures used in the present study (Cho 1990). The relevance of this trade-off to fish in the wild is much more difficult to assess because the daily rations of wild fish can only be estimated based on measurements of instantaneous stomach content and approximate rates of gut clearance (e.g., Boisclair and Marchand 1993) and because these studies typically involve various fish sizes and water temperatures. However, the few available estimates of daily ration among wild juvenile salmonids suggest that the 2.0–4.0% BM·day^{-1} range of rations (and higher, which is important, since naturally occurring food sources would be of lower digestive quality than commercial fish feed) occurs naturally in the wild (Doble and Eggers 1978; Brodeur and Pearcy 1987; Angradi and Griffith 1990), suggesting that this trade-off applies to juvenile trout swimming and growing in the wild as well.

The results of the present study make it clear that individual feeding, growth, and swimming performance are interrelated in a highly complex fashion. Specifically, there is a trade-off between aerobic swimming performance and growth rate that occurs only over a narrow but biologically relevant range of food intakes. In addition, this trade-off appears to result from costs associated with feeding and digestion and cannot be explained simply as a result of the differences in body size or haematocrit associated with rapid growth.

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Interactions among sediments, organic matter, and microbial activity in the hyporheic zone of an intermittent stream

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Abstract: Interactions between surface and subsurface water in intermittent streams are poorly understood. We predicted that surface discharge patterns would influence retention and transport of fine sediments and particulate organic matter in a first-order intermittent stream, which in turn would affect microbial activity at different depths in the sediment. We measured sediments, dissolved and particulate organic carbon, and microbial and bacterial biomass and activity at three depths (surface and 20 and 40 cm) over a period spanning low and high flows at five stations on an intermittent stream. Discharge influenced physicochemical and sediment characteristics at the upstream stations with coarse substratum. In the finer sediments of the lower reaches, an active hyporheic microbial assemblage primarily governed sediment and organic dynamics. With decreasing discharge and increasing retention of fine sediments and particulate organic carbon, greater microbial hydrolytic activity in bed-sediments occurred downstream. Dissolved oxygen, organic carbon, fine sediments, microbial biomass, hydrolytic activity, and bacterial biomass declined with depth, and changed over time, apparently in response to varying discharge. We conclude that discharge and substratum particle size may interact to control organic dynamics and hyporheic microbial activity in a 1st order stream.

Résumé : Il existe peu de données dans la littérature internationale sur les interactions entre les eaux de surface et les eaux souterraines des cours d'eau temporaires. Dans une étude sur un cours d'eau temporaire de premier ordre, nous avons émis l'hypothèse que le débit de surface influence la rétention et le transport des sédiments fins et de la matière organique et donc affecte l'activité microbienne à différentes profondeurs du sédiment. Cinq stations ont été sélectionnées le long du cours d'eau. Nous avons mesuré le volume de sédiments, les concentrations en carbone organique dissous et particulaire et la biomasse et l'activité des communautés microbiennes à trois profondeurs différentes (surface et 20 et 40 cm) et pendant des périodes de hautes et basses eaux. Les caractéristiques physico-chimiques et sédimentaires des stations situées en amont où le substrat est grossier, sont fortement influencées par les variations de débit. La dynamique des sédiments et de la matière organique dans les stations situées en aval où le substrat est plus fin et la zone hyporhéique plus développée, sont principalement contrôlée par l'activité microbienne. Avec une diminution du débit et une augmentation de la rétention des sédiments et de la matière organique, on observe une augmentation de l'activité hydrolytique en profondeur dans ces stations. L'oxygène, le carbone organique, les sédiments fins et la biomasse et l'activité des micro-organismes diminuent avec la profondeur des sédiments et varient au cours du temps en fonction semble-t-il des variations de débit. Ainsi dans la zone hyporhéique d'un cours d'eau de premier ordre, le débit et la taille des sédiments interagissent pour contrôler la dynamique de la matière organique et l'activité des micro-organismes.

Introduction

In temperate regions, small streams often flow below dense canopies, and much leaf litter (coarse particulate organic matter, CPOM) may be retained in their bed, mainly at low water periods during autumn. This litter is first leached, then colonized by microorganisms such as fungi and bacteria, and then consumed by invertebrate shredders and (or) broken down by abiotic abrasion (Cummins 1974). Leaching yields dissolved organic matter (DOM), while shredding and abrasion produce fine and ultrafine particulate organic matter (FPOM and UFPOM). The interface between surface water and groundwater (i.e., hyporheic zone) contributes substantially to the retention and decomposition of organic matter. POM and DOM are stored and transformed by microbial communities in groundwater habitats, which in turn constitute a potential source of nutrients for surface habitats (e.g., Rutherford and Hynes 1987; Ford and Naiman 1989; Fiebig 1995). Geomorphology and hydrology largely determine interactions between surface and interstitial habitats and the permeability of the ecotone in space and time (Gibert et al. 1990; Vervier et al. 1992). In turn, this influences the retention capacity of sediment and biological activity in each system (e.g., Jones and Smock 1991; Webster et al. 1994; Valett et al. 1997). Although this has been studied in mid-order permanent streams, the sedimentary and organic dynamics of intermittent or first-order streams are virtually unknown. Given their collective contribution to the total

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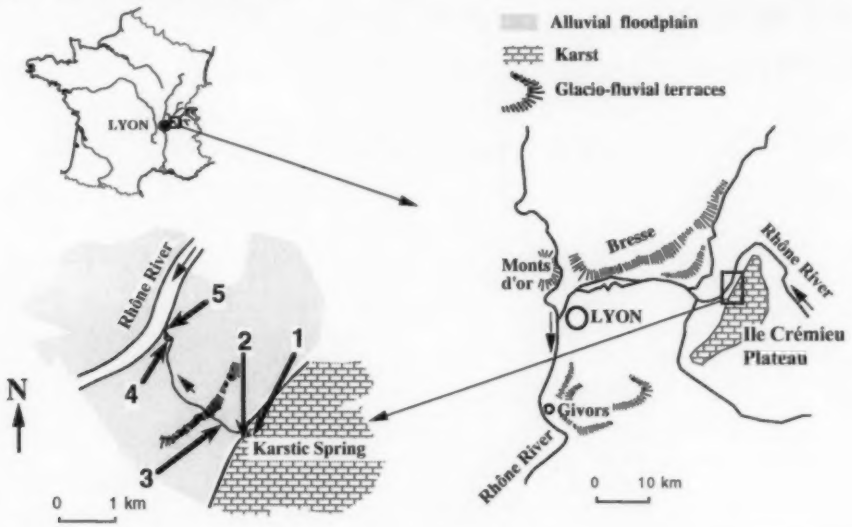
Fig. 1. Location of the study site in France, location of the floodplain of the Rhône River in contact with a limestone massif "Ile Crémieu", and location of stations 1–5 on the stream.



stream network, processes in these feeder streams may influence downstream systems.

The variable flows typical of first-order streams were hypothesized to influence the retention and transformation of sediments and organic matter, in turn regulating the metabolic activity occurring in the hyporheic zone. We predicted that metabolic activity would be greatest in areas of active hydrologic exchange between the surface and hyporheic zones. To test these hypotheses, we sampled water and sediments from different depths at several sites on an intermittent stream emerging from a karstic area. Samples were collected over 8 months of variable surface flow while groundwater flow was permanent, enabling comparisons between different hydrologic conditions.

Materials and methods

Study site

The study site is a braided portion of the floodplain of the Rhône River and its karstic margins, 50 km upstream from Lyon (Fig. 1). The intermittent study stream flows about 2 km towards the Rhone (slope 0.08%) and is the downstream outlet of a karstic spring with a base flow of 50–60 $L \cdot s^{-1}$. Discharge in the downstream part of the tributary is reduced because water is collected for agriculture. At the spring, a gravity and frost-shattered scree spreads out for a few hundred metres, whereas the middle section between the karstic massif and the Rhône River comprises an alluvial terrace for about 50 m (Fig. 1).

Five stations differing in substratum were sampled along this 2-km-long segment. Station 1 was located 4 m inside the cave where water flows through large limestone blocks and cobbles. Station 2 was at the outlet under a mixed tree and shrub canopy with a substratum composed of large pebbles and cobbles. Station 3 lay about 40 m downstream from the outlet, under an open canopy and with a cobbles–gravel substratum. Stations 4 and 5, both close to the Rhône and only 30 m apart, were located in the alluvial floodplain under closed riparian canopies bordered by corn and sunflower fields. Station 4 was an interstitial spring 100 m upstream from the Rhône River. Station 5 was located in the tributary about 30 m downstream from station 4. Water flowed over gravel sediments, and small gravel deposits were observed at this station.

Hydrological measurements

Hydrological measurements included surface discharge and inputs of precipitation on the catchment. Instantaneous flow was manually measured at station 3 during the sampling period. Rainfall was monitored with an automated rain gauge in the Courtenay meteorological station (National Meteorology) located 10 km southeast of the study area. Stations were sampled monthly from December 1989 through July 1990.

Physical, chemical, and biological measurements

At each station, three points were sampled for surface and groundwaters and sediments. Water and sediments were collected with a 1-L corer from the surface and with perforated metal piezometers from 20 and 40 cm below the sediment surface for subsurface samples.

Groundwater chemistry was measured on water pumped directly from the piezometers using a peristaltic hand pump (W.A. Bachofen type). For sediment characteristics (organic matter content and biofilm parameters), water and fine sediments (<5 mm) were collected using a Bou-Rouch pump (Bou and Rouch 1967; Bou 1974) connected to the piezometers. Only sediments <1 mm were considered because this fraction was predominant in the samples.

Temperature, specific conductance, dissolved oxygen, and pH were measured directly in the field with a thermoconductimeter (LMC model CM 85 T), an oxymeter (LMC model OXY 85 T), and a pH meter (LMC model pH 85, WTW electrodes). Water (10 mL) was filtered on a glass fiber filter (0.7 µm, no surfactant) for dissolved organic carbon (DOC) determination. In the laboratory, DOC concentration was measured with a Dohrman DC 80 analyser based on UV-promoted potassium persulfate oxidation (precision ± 1%) after previous elimination of mineral carbon by orthophosphoric acid (1 $\mu L \cdot mL^{-1}$) and carbon dioxide stripping under a 10-min oxygen flow.

Sediments were separated into two size fractions, fine sediments (FS) between 50 µm and 1 mm and very fine sediments (VFS) <50 µm, by wet sieving. Particulate organic carbon contents in FS and VFS (FPOC and VFPOC) were measured with a Dohrman DC

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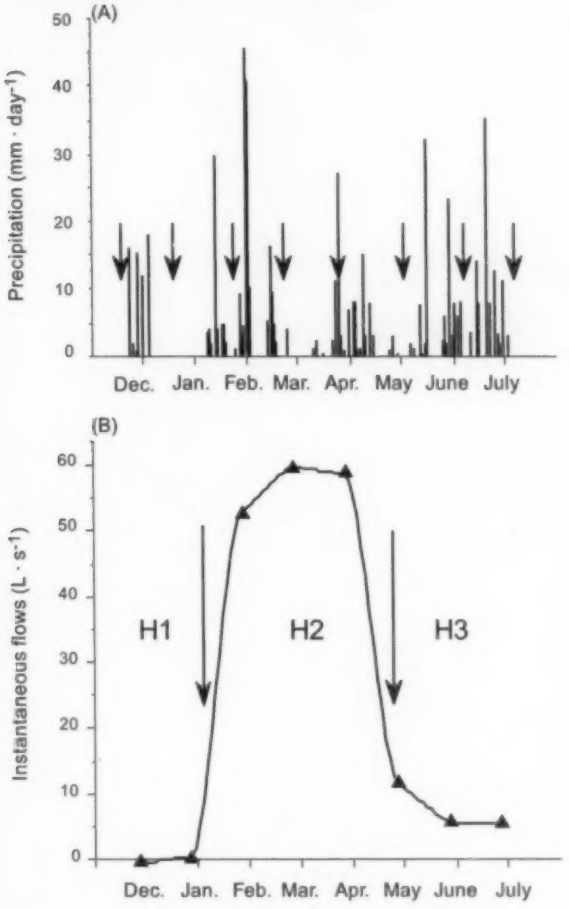

Fig. 2. (A) Daily rainfall measured at the Courtenay meteorological station located 10 km southeast of the study site. Arrows indicate the sampling dates. (B) Instantaneous flow measured at station 3 during the sampling period. Hydrologic periods: H1, low water (December–January); H2, high water (February–April); H3, low water (May–July).

80 carbon analyser fitted with a sludge–sediment sampler using combustion at 850°C with cobalt oxide on aluminium as a granular catalyst. Organic matter associated with the sandy fraction (<1 mm) was dispersed in a sonic bath, centrifuged, and ground before analysis.

Biofilm parameters were determined on the fine sediments (<1 mm) pumped by the Bou-Rouch method (Bou and Rouch 1967). Total bacteria were enumerated under an epifluorescence microscope (Olympus BH-2, fitted with a 200-W mercury burner and an Olympus UG-1 365-nm excitation filter) after 4′,6-diamidino-2-phenylindole (DAPI) staining (e.g., Fry 1988). Wet sediments (<1 mm, 1 g) were mixed with 50 mL of filtered distilled water (0.2-µm acetate membrane) and sonicated (Vibracell 375) for 180 s (power 2, duty cycle 50%) to remove bacteria from the sediment. The suspension (10 mL) was filtered on a Whatman glass fiber filter (GF/D type, mesh 2.7 µm) to eliminate the coarsest particles. The filtrate (1 mL) was transferred to a 10-mL filtration unit fitted with a GTBP Millipore membrane (mesh 0.2 µm) together with 1 mL of a 4 mg DAPI·L^{-1} solution. After 10 min, the suspension was filtered. The filter was then washed and mounted in nonfluorescent oil on a microscope slide for counting. Bacterial numbers were converted into biomass using a conversion factor of 308 µg C·μm^3 bacterial $volume^{-1}$ (Fry 1988).

Total microbial biomass was also approximated by estimating the DNA concentration of the sediment using the diphenylamine method (Dische method modified by Burton 1956) after xylene extraction (Fontvieille and Fevotte 1981). Nucleic acid extract (1 mL) was mixed with 2 mL of diphenylamine reagent and heated for 10 min in boiling water. The mixture was then filtered on a Whatman glass fiber filter (GF/F type, 0.7 µm) and optical density of the filtrate was read at 598 nm. The organic phosphorus (phosphate group) content of DNA was read as reference rather than DNA weight so that DNA samples of varying degrees of purity would yield the same curve when diphenylamine color intensity was plotted against DNA-P.

Microbial hydrolytic activity was measured by the fluorescein diacetate (FDA) method. This is a rapid colorimetric method easy to apply for a global estimate of metabolic activity in sediments (e.g., Köster et al. 1991; Fontvieille et al. 1992). FDA solution (0.1 mL) was directly added to 1 g of wet sediments (<1 mm) together with 3 mL of phosphate buffer solution (pH 7.6). The incubation was maintained at 11°C for 60 min in the dark. The reaction was stopped by freezing (–20°C) the sediment after 3 mL of a $HgCl_2$ solution (400 mg·L^{-1}) was added. Fluorescein concentration was estimated from the optical density of the filtered supernatant (0.45-µm acetate membrane) measured at 490 nm (Unicam-SP1800-UV spectophotometer). Results were expressed as micromoles of hydrolyized FDA per hour per litre of sediment.

Data analysis was performed using the Statistica/W statistical package (version 5.0, StatSoft Inc.). Water and sediment characteristics (FS and VFS), organic carbon fractions (DOC, FPOC, and VFPOC), and biological characteristics (bacterial and microbial biomass and hydrolytic activity) were compared spatially (between stations and depths) and temporally using Kruskal–Wallis tests. This nonparametric test was chosen because of the heterogeneity of the variances of most variables. A $\log(x + 1)$ transformation of all parameters was used to normalize data prior to a Pearson's correlation analysis between sediment content, nutrient concentrations (DOC and POC), and biological characteristics.

Results

Hydrological periods

Hydrologic measurements (daily precipitation and instantaneous flows) revealed three hydrologic periods during the study (Fig. 2). A dry period (H1), characterized by low discharge (<1 L·s^{-1}), occurred from December (total rainfall 64 mm) to January (49 mm). A slight increase in piezometric level was recorded in January at the cave outlet, which then began to overflow to the surface. A high-flow period (H2) began in February (total rainfall 157 mm) and lasted until April (102 mm). During this period, a spate occurred at the cave outlet with a peak in March (Fig. 2); the downstream station (5) was flooded by the Rhône. The last period (H3) began in May when rainfall decreased (total rainfall 15 mm). Low discharge persisted in June and July despite frequent storms during these months (Fig. 2), due to the underground origin of the stream and the loss of water by evapotranspiration.

Spatial and temporal variations of water characteritics

Water temperature was higher in the cave (station 1) during the first hydrological period H1 than at stations 2 to 5 ($P < 0.05$) at all depths. At these stations, the lowest values

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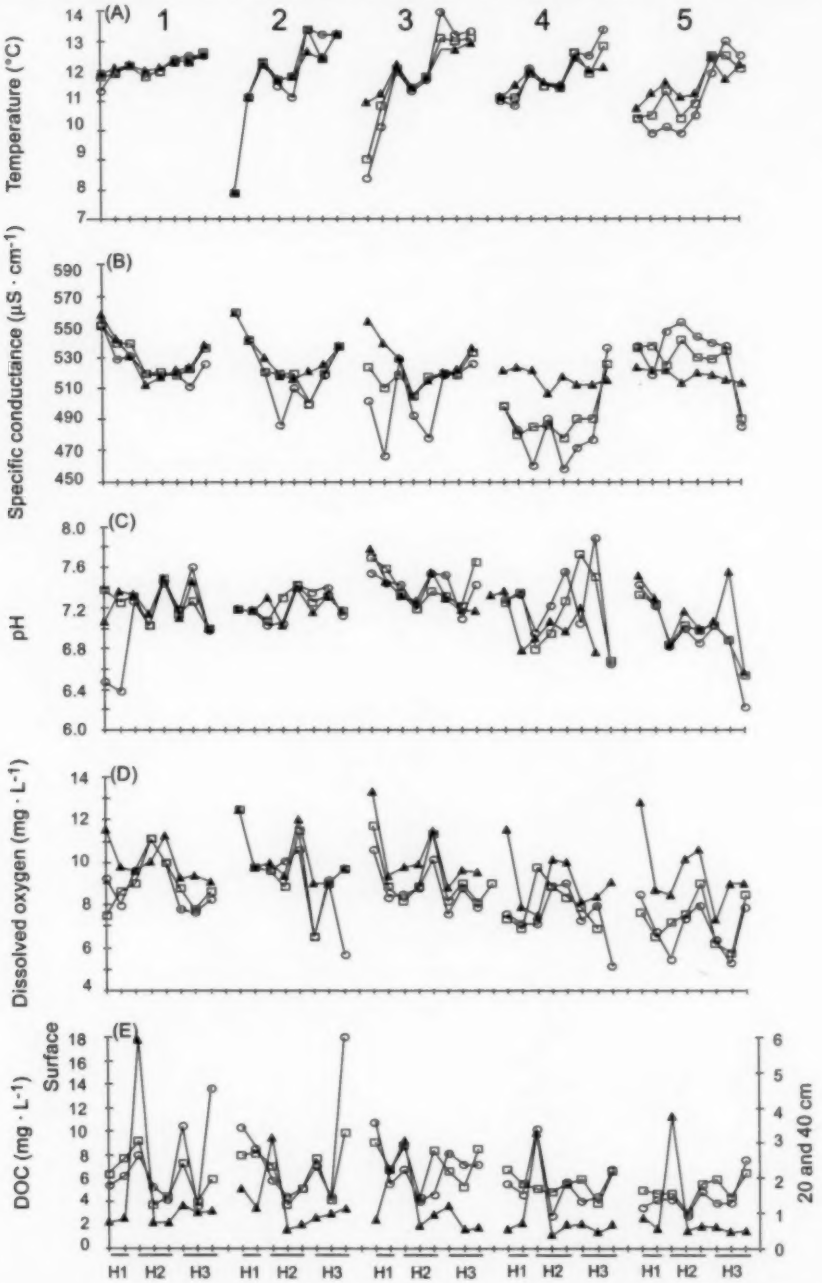
Fig. 3. Water characteristics at stations 1–5 at each depth (▲, surface; □, 20 cm; ○, 40 cm) and for each hydrological period (H1, low water (December–January); H2, high water (February–April); H3, low water (May–July)).



were measured in December (7.9°C at the cave outlet, when a fine layer of snow covered the ground), but the temperature range between the H1 and H3 periods never exceeded 4°C (Fig. 3). Water was well mineralized (about 500 µS·cm^{-1}) during all hydrological periods (Fig. 3), although a slight but significant decrease was observed during the high-discharge period (H2) at stations 1 and 2. Station 4 had lower specific conductance than the other stations ($P < 0.05$) and conductance decreased with depth. In contrast, at station 5, mineralization significantly increased from the surface to 40 cm deep. Water was slightly basic at all stations, except at station 5, where pH fell under 7 during H2 and H3 and with depth (20 and 40 cm deep below the sediment surface) ($P < 0.05$).

Stations 4 and 5 were significantly less oxygenated than

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Fig. 4. Sediment and POC fractions at stations 1–5 at each depth (▲, surface; □, 20 cm; ○, 40 cm) and for each hydrological period (H1, low water (December–January); H2, high water (February–April); H3, low water (May–July)).

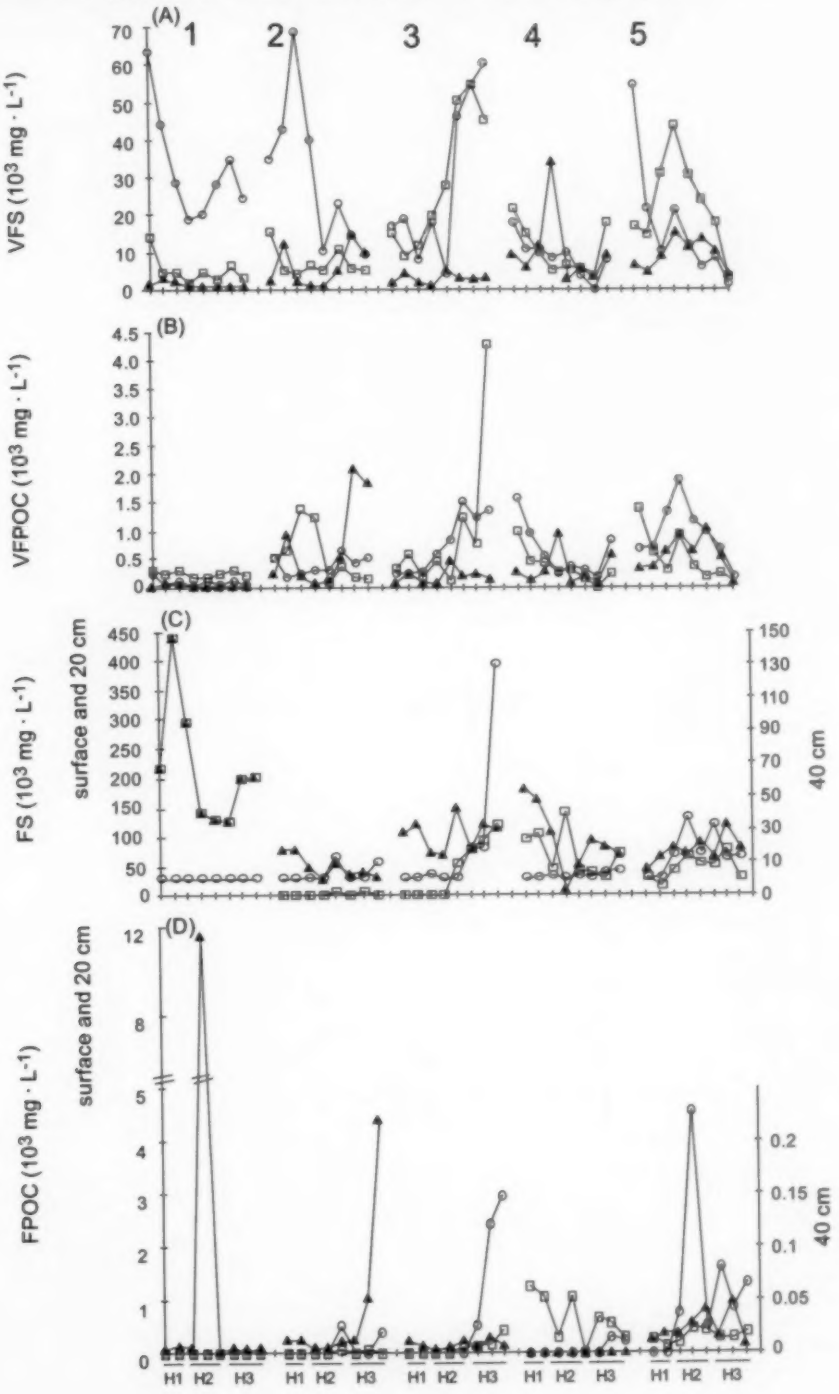

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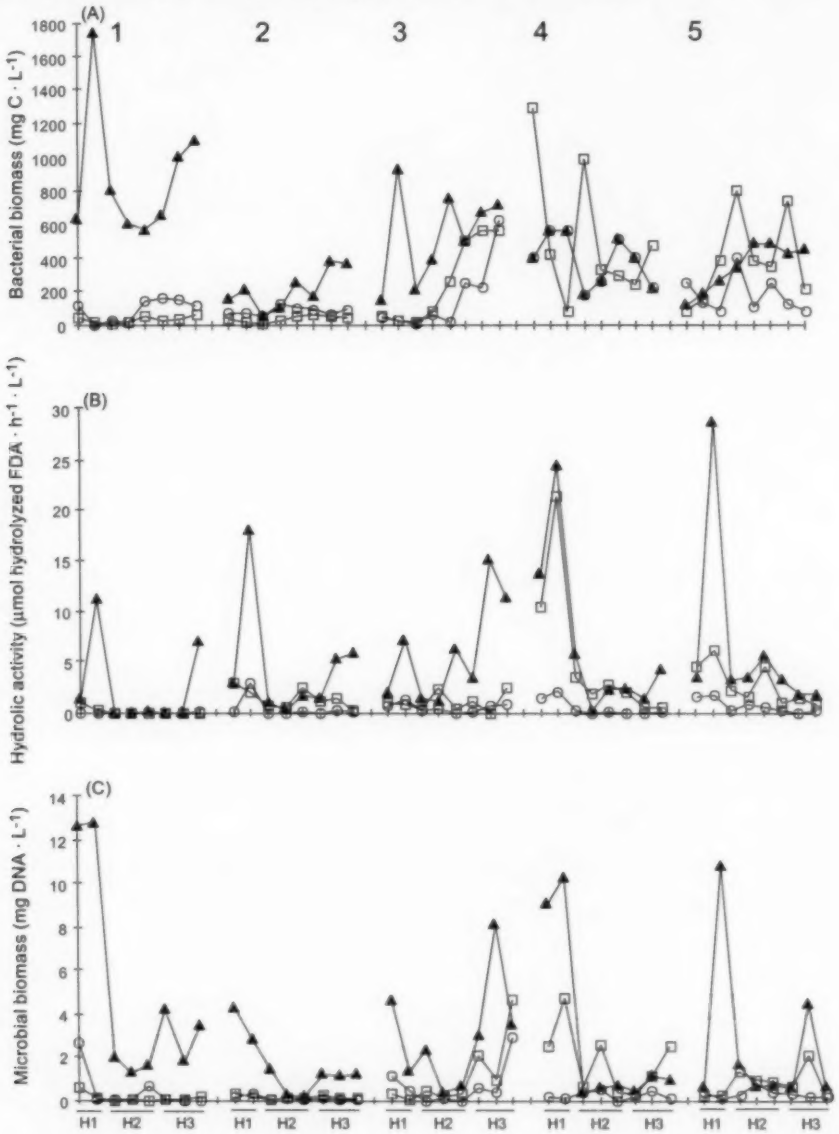
Fig. 5. Biofilm characteristics at stations 1–5 at each depth (▲, surface; □, 20 cm; ○, 40 cm) and for each hydrological period (H1, low water (December–January); H2, high water (February–April); H3, low water (May–July)).



the other three stations ($P < 0.05$), especially at 20 and 40 cm depths (Fig. 3). At station 1, oxygen concentration peaked during H2, while stations 2 and 3 were more oxygenated during the low-flow period H1. DOC concentration was significantly higher at the upstream stations than at stations 4 and 5 during the low-flow periods H1 and H3. DOC concentration varied temporally at all stations, with a peak in February (Fig. 3). Differences between hydrologic periods were significant only at station 3.

Sediment characteristics and organic carbon fractions

Stations 1 and 2 had significantly less VFS and VFPOC than the other stations at all depths ($P < 0.05$). A similar pattern was observed for the fine fractions FS and FPOC but was only significant during the high-discharge period H2 and at 20 and 40 cm depths (Fig. 4). At station 1, there were significantly higher levels of VFS and VFPOC at 40 cm than at the surface and 20 cm. Fine fractions (FS and FPOC), however, were restricted to the surface regardless of the hydrological period. At station 2, very fine fractions (sediment and POC) also significantly increased with depth. In contrast, FS decreased between the surface and 20 cm ($P < 0.05$) during all periods and slightly increased at 40 cm during the H2 and H3 periods. At station 3, VFS and VFPOC accumulated at 20 cm for all periods ($P < 0.05$). The fine fractions (FS and FPOC) significantly increased during the

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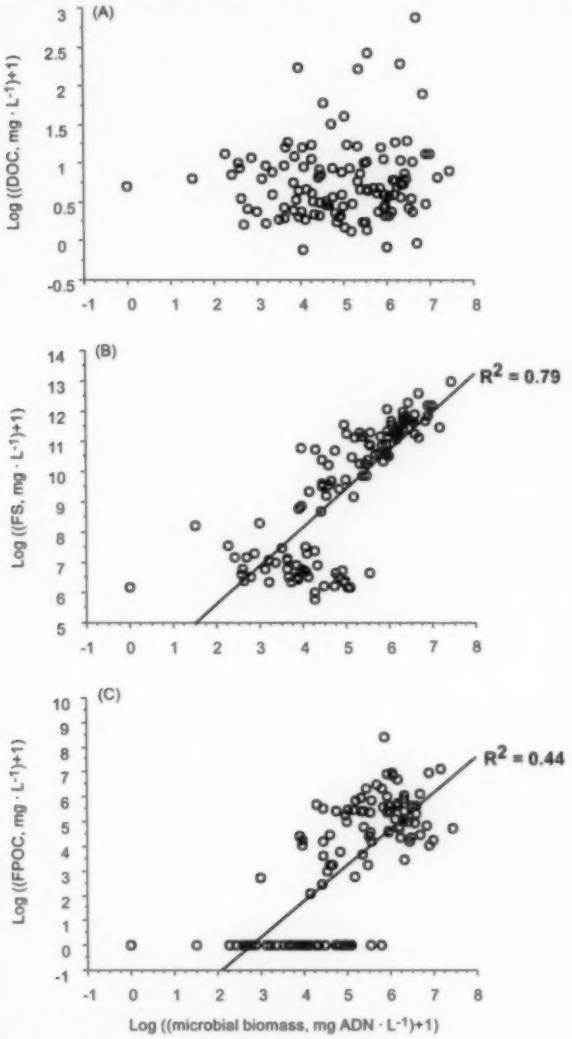
Fig. 6. Pearson's correlations between microbial biomass and (A) DOC, (B) FS, and (C) FPOC. Similar Pearson's correlations existed (not shown) between bacterial biomass and FS (R^2 = 0.79) and FPOC (R^2 = 0.41) and between hydrolytic activity and FS (R^2 = 0.59) and FPOC (R^2 = 0.65) ($P < 0.01$).



H3 period, especially at depths of 20 and 40 cm, accounting for the lack of vertical pattern during this period. At station 4, VFS content peaked during the H1 period at 20 and 40 cm, but very fine fractions (VFS and VFPOC) did not vary with depth at any period. In contrast, FS and FPOC accumulated in the first 20 cm of sediment. At station 5, VFS and VFPOC were abundant, especially in the bed sediments, while FS and FPOC decreased with depth ($P < 0.05$) during all periods.

Biological characteristics

Microbial and bacterial biomasses and hydrolytic activity were significantly higher at the surface than in the sediments, regardless of station, when all hydrologic periods were considered together (Fig. 5). At station 1, microbial and bacterial biomasses at the surface exceeded those at the other stations ($P < 0.05$) during all periods. In contrast, biomass and hydrolytic activity in the riverbed sediments were greater at stations 4 and 5 than at the other stations, especially during the two first hydrological periods. At station 3, microbial and bacterial biomasses increased during the H3 period at all depths.

Dissolved oxygen content correlated negatively with very fine fractions of both sediment (R^2 = –0.27) and organic carbon (R^2 = –0.20) ($P < 0.05$). In contrast, no significant relationships were observed between the other physicochemical and biological variables (biomasses and activity) ($P > 0.05$). DOC displayed no significant relationships with biological variables ($P > 0.05$), whereas significant relationships existed between sediment, POC concentration, and biological characteristics (Fig. 6). All biological variables correlated positively with FS at all stations, depths, and periods. Biomasses and activity were also significantly related to FPOC, but only in the sediments (Fig. 6). Bacterial biomass was negatively correlated with VFS fraction during the H1 period, probably because of the marked reverse vertical pattern of these two variables (R^2 = –0.51, P = 0.004).

Discussion

In this study, DOC and dissolved oxygen concentrations declined downstream in the alluvial floodplain, as reported for other low-order streams (Kaplan et al. 1980; Dahm 1984), and varied with hydrological period. Processes regulating DOC content in subsurface waters are complex (e.g., Findlay at al. 1993). Leaf leachates and soil layers contribute most of the DOC to the surface waters at the head of the tributary, especially during the winter low-flow conditions. DOC content is changed by both physical mechanisms (e.g., adsorption onto sediments or the biofilm matrix; Freeman et al. 1995; Marmonier et al. 1995) along the stream and biological processes (decomposition and consumption by microorganisms). In this study, there was no statistical relationship between biofilm parameters and DOC concentration, as described previously for the hyporheic zone (Bärlocher and Murdoch 1989).

Two hypotheses can be proposed. First, the quality of DOC may be more important to microbial communities than simply DOC quantity. The simultaneous increase in DOC concentrations with discharge could be due to the accumulation of leachates as well as to changes in flow paths (Mulholland et al. 1990; Hornberger et al. 1994). As other authors have observed, variable DOC inputs in response to changes in water flow (e.g., Vervier and Naiman 1992) or inputs from different soil horizons (Easthouse et al. 1992) probably import different-quality DOC (i.e., relative proportions of biodegradable and refractory fractions into the DOC pool). Second, as DOC is abundant (>1.5 mg·L^{-1}) in this system, POC may be the limiting factor, as is often observed in natural environments (Billen 1991; Turley 1994).

In this way, organic and inorganic fine particles may govern microbial and bacterial biomass and activity. However, the vertical distribution and the effect of increased discharge on patterns of FS, POC, and biological characteristics in the

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different stations probably reflect different influences on microbial functioning in the hyporheic zone.

In the cave and at its outlet (stations 1 and 2), which are characterized by large pebbles and fed by karstic groundwater poor in organic nutrients, microbial processes are associated with surface regions where FS settle during the cold low-flow period. Hence, increases in discharge have the greatest effect on the surface compartment. All fractions at the surface (fine and very fine) were washed away during high-flow periods, and biomass and activity decreased due to the sensitivity of sessile microbial communities to scouring. Similarly, Snaddon et al. (1992) observed that POM deposited on the sediment surface is removed by high flow. This is in contrast with deeper layers, where sediment and POC contents vary slightly or even increase with depth but without stimulating the microbial community. The conditions observed during the first low-flow period seemed to be restored rapidly after the disturbance, mainly due to sediment and associated POC inputs from groundwaters to the surface. Thus, system functioning may be mainly controlled by physical processes.

In the alluvial floodplain (stations 4 and 5), physicochemical characteristics reflect the influence of interstitial water from the Rhône River that circulates through the sediments of the alluvial floodplain. At these stations, microbial processes are not restricted to the surface, as FS and associated POC are present to a depth of 20 cm and support a well-developed biofilm. Increased discharge brings sediments (fine and very fine) and associated POC fractions into the riverbed. A high microbial biomass and hydrolytic activity is maintained, leading to efficient nutrient cycling. Consequently, system functioning seems to be dominated by biological processes. The lack of sediment erosion and POC during high water is because of sediment deposits that trap particles. However, the stimulation of biological processes by nutrient inputs as well as high VFS content led to the decrease in oxygen content and pH during the summer period. These conditions, associated with a limited exchange of water, probably induced a decrease in microbial activity in the sediments, affecting the biological control of the system.

Station 3 displayed variable physical characteristics with mixed coarse sediments and FS and a combined influence of groundwater underflow and surface water. The vertical distribution of sediments, POC, and microbial communities was highly modified by the discharge increase. Slight changes were observed at the surface, with a decrease in FS and biomasses (microbial and bacterial) as well as in activity. The increase in discharge enhanced sediment (fine and very fine) and VFPOC transport into the riverbed (at 20 cm) from the surface (Naegeli et al. 1995). This promoted microbial biomass and activity, which increased during the summer low-discharge period. Thus, at this station where exchanges between surface and interstitial habitats are well developed, two types of processes control system functioning. Increases in discharge seem to enhance permeability into bed sediments (a physical process), in turn promoting better POM decomposition (a biological process) at all depths and improving the self-purification capacity of this station.

In conclusion, sediment and POC dynamics are the major factors that control microbial processes at the surface and in the shallow hyporheic zone in this stream. The influence of discharge on retention and transformation of material varied among stations, even within such a small stream (<5 km). The discharge increase seemed to favor microbial activity in reaches with a well-developed shallow hyporheic zone (stations 4 and 5) or with potential exchanges with the surface (station 3). In contrast, a decline in microbial activity was observed in reaches where surface processes predominated and sediments were coarse (stations 1 and 2).

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Age characteristics of coarse woody debris (*Pinus strobus*) in a lake littoral zone

Richard P. Guyette and William G. Cole

Abstract: Littoral coarse woody debris (CWD) is a persistent class of aquatic habitat that accumulates over many centuries and provides habitat for diverse floral and faunal communities. We used dendrochronological methods to analyze residence times and age-related characteristics of eastern white pine (*Pinus strobus*) CWD in the littoral zone of Swan Lake in Algonquin Provincial Park, Ontario. The mean calendar date of all the annual rings in CWD samples was 1551. Annual rings dated from calendar year 1893 to 982. The mean time from carbon assimilation in a live tree to carbon loss from littoral woody debris was 443 years. Outside ring dates of the woody debris were significantly correlated with the bole's maximum and minimum diameter ratio, mass, specific gravity, length, and submergence. Negative exponential functions described the temporal structure of the CWD mass and abundance. Accelerated inputs of woody debris resulted from late nineteenth century logging and a disturbance circa 1500. No mature eastern white pine have fallen into the lake over the last 100 years.

Résumé : Les gros débris ligneux riverains qui s'accumulent dans l'eau près des rives durant des siècles constituent un habitat aquatique persistant qui abrite diverses communautés végétales et fauniques. Nous avons utilisé des méthodes dendrochronologiques pour analyser les temps de résidence et les caractéristiques liées à l'âge des gros débris ligneux de pin blanc (*Pinus strobus*) dans la zone riveraine du lac Swan, dans le parc provincial Algonquin, en Ontario. La date du calendrier moyenne de tous les cernes dans les échantillons de gros débris ligneux était 1551. Les cernes dataient des années 1893 à 982. Le laps de temps moyen depuis l'assimilation du carbone dans un arbre vivant jusqu'à la déperdition de carbone par les débris ligneux riverains était de 443 ans. Les dates des cernes extérieurs des débris ligneux étaient significativement corrélées avec le rapport des diamètres maximum et minimum, la masse, la densité, la longueur et la submersion des fûts. Des fonctions exponentielles négatives ont permis de décrire la structure temporelle de la masse et de l'abondance des gros débris ligneux. Il y a eu accélération de l'accumulation de débris ligneux par suite de la coupe de bois à la fin du dix-neuvième siècle et d'une perturbation survenue vers 1500. Aucun pin blanc mûr n'est tombé dans le lac au cours des 100 dernières années.

[Traduit par la Rédaction]

Introduction

Coarse woody debris (CWD) is present in the littoral zone of many of the nearly 260 000 lakes in Ontario. Little is known, however, about its residence time, spatial distribution, and time-related characteristics in littoral zones. CWD is particularly abundant in small, undeveloped, oligotrophic lakes where dense forest patches dominate the land–water ecotones. Littoral zone CWD provides an important substrate for many plant and animal species in the forest–lake ecotone (Bowen et al. 1995; France 1997), as well as helping to protect shoreline soil and vegetation from wave and ice erosion. The Ontario Ministry of Natural Resources (OMNR) estimates that as much as 90% of all lake biota depends on the littoral zone for its survival (OMNR 1994). About two thirds of the world's commercially harvested fish species use aquatic ecotones for spawning, cover, feeding, or nursery habitat (Mitsch and Gosselink 1986). Young brook trout (*Salvelinus fontinalis*) and other fish species often rely on shoreline CWD for protective cover (Tabour and Wurtsbaugh 1991; Biro and Ridgway 1995). CWD provides a refuge from predation in many aquatic habitats (Everett and Ruiz 1993). It also contributes an unknown but possibly significant amount of dissolved organic carbon into lake waters (Bowen et al. 1995; McCart et al. 1995) and may serve as a significant landscape-level carbon sink (OMNR, Peterborough, Ont., unpublished data). Considerable information is available on the ecology of CWD in forest streams (Harmon et al. 1986; Andrus et al. 1988; Bilby and Ward 1991; Maser and Sedell 1994); however, much less is known about its ecological function in lake environments (Pieczyñska 1990; Christensen et al. 1996).

There is a deficiency of information on which to base policies about CWD in lake littoral zones. The current Department of Fisheries and Oceans (DFO 1986) guidelines do not make specific recommendations on CWD management. Although OMNR guidelines for aquatic habitat protection and timber management (OMNR 1988, 1991, 1994, 1998*a*, 1998*b*) strongly discourage any logging activity within a 30- to 90-m buffer strip and prohibit the deposition of any logging debris in or near the water, they state that "limited amounts of large debris may benefit fish habitat provided that the debris is stable". More knowledge concerning the distribution, spe-

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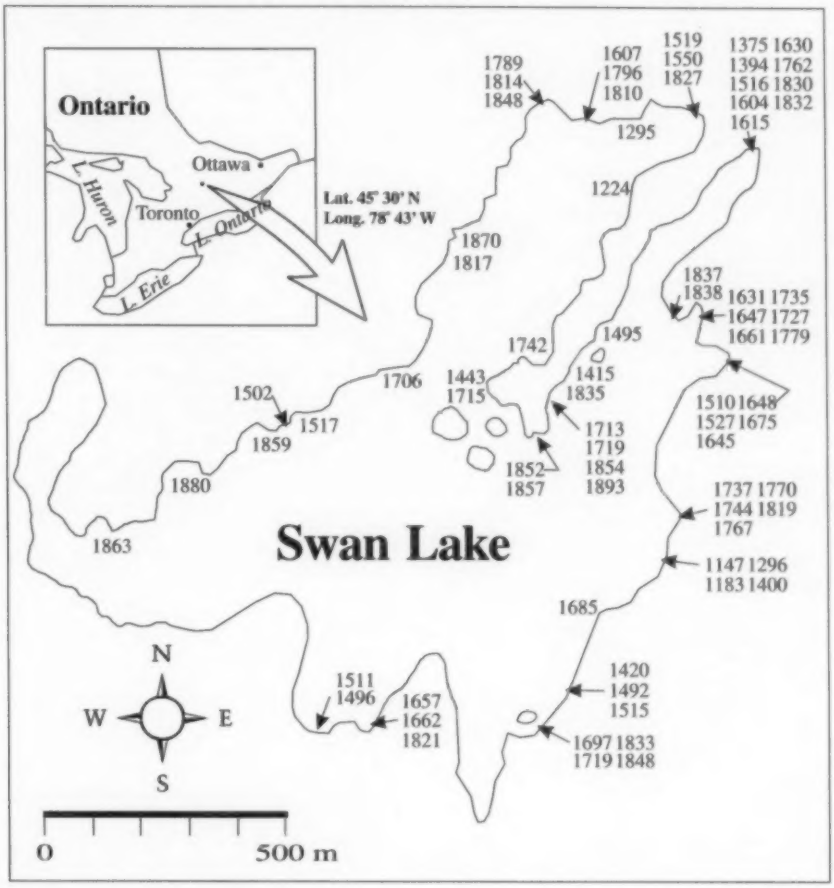
Fig. 1. Spatial distribution of the eastern white pine CWD in the littoral zone of Swan Lake, Algonquin Provincial Park, Ontario. Approximate locations of CWD pieces are given by their outside ring dates.



cies, and age-related characteristics of littoral CWD will provide a better understanding of the coupling of adjacent terrestrial and aquatic systems that can be used for the management of CWD additions or removal during lakeshore development, fish habitat alterations, and timber harvesting.

The objectives of this study were to (*i*) estimate the residence times, age structure, and decay rate of eastern white pine (*Pinus strobus*) CWD in the littoral zone of an oligotrophic lake in south-central Ontario using dendrochronological dating, (*ii*) describe age-related characteristics of littoral zone CWD, and (*iii*) establish methods for sampling, processing, and dating CWD in littoral zones.

Methods

Swan Lake is located in Algonquin Provincial Park, Ontario, Canada (78°43′W, 45°30′N), elevation 436 m above sea level (Fig. 1, inset). The lake has about 9.5 km of shoreline and has a surface area of 87 ha. The littoral zone substrate is primarily a gently sloping bottom with fine, deep organic sediment, with some inclusions of gently sloping sandy bottoms and steep, shallow monolithic rock outcrops that are part of the underlying Precambrian Shield bedrock. Swan Lake is oligotrophic, clear, and slightly acidic (pH = 6.4). The lake is normally ice free from late April until late November.

The forest stands surrounding Swan Lake comprise tolerant northern hardwoods dominated by sugar maple (*Acer saccharum*), yellow birch (*Betula alleghaniensis*), American beech (*Fagus grandifolia*), and red maple (*Acer rubrum*). Like many other small lakes in this region of Ontario, Swan Lake is surrounded by a discrete coniferous forest zone that often overhangs the shoreline and extends up to 30 m inland, with a fairly abrupt edge between this zone and the surrounding upland hardwood forest. Dominant tree species in this ecotone include eastern white pine, eastern hemlock (*Tsuga canadensis*), eastern white-cedar (*Thuja occidentalis*), balsam fir (*Abies balsamea*), spruce (*Picea* spp.), and tamarack (*Larix laricina*). The two most common species of large logs in the littoral zone of Swan Lake are eastern white pine and eastern hemlock.

Swan Lake has no shoreline cottage development, but the entire watershed was logged one or more times in the late nineteenth and early twentieth centuries for eastern white pine, eastern hemlock, and high-quality yellow birch. During the late nineteenth century, all merchantable eastern white pines, including those in the forest–lake ecotone, were harvested and rafted to the northeast arm of the lake and then down the outflow to the next lake (Fig. 1).

Eastern white pine was chosen for this study because (*i*) it is abundant as CWD in the littoral zone, (*ii*) it is one of the most dominant tree species in the terrestrial shoreline ecotone of many

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lakes in Ontario, and (*iii*) it has the dendrochronological characteristics required for tree-ring dating such as solid wood, few false or missing rings, and sufficient year-to-year high-frequency ring-width variability.

Samples were collected from 102 logs from the littoral zone (<3 m from shore and <3 m deep) of Swan Lake. Our sampling was not random. We attempted to sample only eastern white pine and collected samples from nearly all of the large eastern white pine woody debris in the littoral zone of the lake. Of the 102 logs sampled, 92 were eastern white pine. The remaining logs were eastern hemlock and were omitted from subsequent analyses. We did not collect samples from CWD with cut ends (four logs) or from CWD that had fewer than about 100 annual rings (11 logs). Visible log characteristics (e.g., log length, diameter, branching pattern, wood texture, and buoyancy) were used to distinguish eastern white pine CWD from the CWD of other tree species in the littoral zone. For each piece of CWD, we measured the total length of each log, estimated the percentage of total log length under water, noted the surface texture class of the log (rough or smooth), and noted the location and orientation of the log along the lakeshore.

A 3000-kg hand winch and rope were secured to a shoreline tree and used to raise logs to the surface and to move them to shallow water for cutting. A cross-sectional disk was cut with a chainsaw from each log while in shallow water. We selected the section of log to sample by three criteria: the section with the largest diameter, the section with the most solid wood, and the section closest to the lower end of the bole as possible. This maximized the number of rings (for both cross-dating and outside ring determination) and minimized the difference between pith dates and tree germination. Fifty-nine percent of the cross sections were cut from the main bole of the former trees and 41% came from near the crown base, estimated from branch stub densities and angles.

Cross sections were labeled with paint markers, photographed, and measured for minimum and maximum diameters of the cross section (centimetres). Tape was used to keep some of the cross sections intact and complete during transport and processing. Wedges were cut from the cross sections, air-dried, and then sanded to reveal the cellular detail of each annual ring to facilitate species identification, tree-ring dating, and ring-width measurement.

Dendrochronological methods were used to date the eastern white pine CWD. We measured the width of annual growth rings along the radial axis with the highest year-to-year high-frequency ring-width variability, the largest number of rings, and the least amount of nonclimatic ring-width variability. Nonclimatic ring-width variability was minimized by selecting radii that excluded suppressed and abrupt changes in ring-width series due to reaction wood, bole geometry, and stand dynamics. Ring-width plots were made, compared on a light table, and matched visually. In addition to visual matching of ring-width plots, comparisons of late wood characteristics and prominent narrow ring sequences were made (Stokes and Smiley 1968). Statistical verification of the ring-width series and dating was done using COFECHA (Holmes 1986; Grissino-Mayer et al.1996) and Student *t* tests (Baillie 1982). Nonclimatic ring-width variability was also minimized at this stage by calculating ring-width indices by dividing the actual ring widths by a smooth curve fit to the ring-width series (Fritts 1976).

CWD samples were first cross-dated with each other to build a floating chronology (i.e., not linked to known calendar years) and then dated in absolute time by cross-dating with tree-ring chronologies derived from living, old-growth eastern white pine at Dividing Lake (Guyette and Dey 1995), 13 km southeast of Swan Lake, and Hobbs Lake, 140 km northwest of Swan Lake. The Dividing Lake old-growth chronology was 333 years long (dating to 1661) and the Hobbs Lake old-growth chronology was 447 years long (dating to 1547). These chronologies overlapped the Swan Lake chronology by more than 200 years and dated the Swan Lake chronology in absolute time. The ring-width data and chronologies for eastern white pine at Dividing and Hobbs lakes are on file in the International Tree-Ring Data Bank of the World Data Center-A for Paleoclimatology in Boulder, Co. (Guyette 1996*a*).

The outside ring dates of the CWD were used as proxies for the time of tree death. This method biases the actual date of tree death and the rate of the depletion of logs from the lake toward slightly more ancient dates. Since in most cases, some annual rings were missing from the outside of the CWD, the actual date of tree death is not as ancient as the proxy date or outside ring date. Here, we present the raw data and discuss the magnitude of this bias.

Two subsamples of wood from each disk were oven-dried to determine the relationship between wood specific gravity and outside ring age. We avoided using compression wood, discolored wood, and decayed wood in this analysis. Thus, we determined the specific gravity of what appeared to be wood unaffected by decay and weathering, not whole-log specific gravity, which would have been less. Each CWD sample's oven-dry specific gravity was calculated by dividing the dry weight of each subsample by its oven-dry volume. The volume of the sample was measured by the volume of water that it displaced.

Since CWD length and diameter measurements were made on wet wood, mass calculations were multiplied by a volume shrinkage coefficient of 0.92 (Panshin and de Zeeuw 1970) and multiplied by the oven-dry specific gravity from each log's respective sample to calculate the dry mass of the logs. A rough estimate of the dry mass for each log was calculated as

$$\text{log mass} = (\text{mean radius})^2 \times \pi \times \text{length} \times \text{specific gravity} \times \text{shape coefficient}$$

where the shape coefficient is either 0.6 for logs approximated by a partial cone or 0.9 for logs with a cylindrical shape.

Negative exponential functions were used to quantify the dependence of both the cumulative mass of CWD and the cumulative frequency of CWD on time (outside ring dates). These equations are descriptive, since the amount and structure of CWD through time are the result of unknown rates of both decay and input. Little is know about input rates that can vary greatly due to natural disturbances, the age distribution of shoreline eastern white pine, and logging. The descriptive functions were fit to the outside ring dates of the CWD. However, because no logs have fallen into the lake over the last 100 years (and thus no data points), this descriptive function is limited to CWD with outside ring dates greater than 100 years BP. The equations were fit by iterations of the exponential constant, starting at times defined by an approximate half-life and yielded decay constants ($-k$) of the quantities. We then derived coefficients using the exponential term $\exp^{-kt}$ in nonlinear least squares regression routines.

Results

Dendrochronological methods were found to be an excellent way to describe the age structure of CWD habitat (Fig. 2). The length of the eastern white pine tree-ring series (mean 213 years, Table 1) and the mean between-tree series correlation of 0.54 ($p < 0.001$) enabled us to date more than 89% of the eastern white pine CWD samples. The collection of cross sections also greatly improved dating because of our ability to select a ring-width series with good dating characteristics such as clear distinct annual rings, maximum series length, solid wood without decay, and the lack of compression wood. Inner portions of the ring-width series were consistently less well correlated among trees than were the middle

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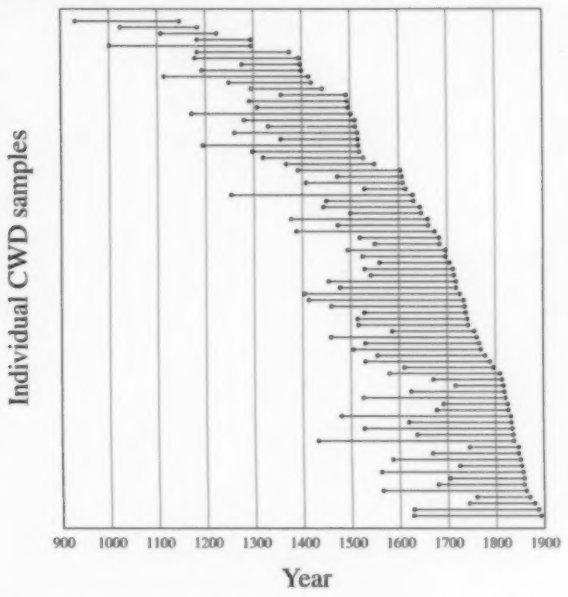
Fig. 2. Age and residence time of eastern white pine CWD in the littoral zone of Swan Lake. CWD is sorted by ascending outside ring date. Bar length is proportional to the number of growth rings in the sample (i.e., tree's minimum life span).



and outer sections of the tree-ring series. CWD from Swan Lake dated over a period of 911 years from 982 to 1893 and extended 1014 years BP. Older CWD probably exists in Swan Lake but is buried in littoral sediment or in lakeshore bogs or is in deeper water and was beyond the scope of our habitat-related project. The eastern white pine ring-width measurements and chronology for Swan Lake are registered with the World Data Center-A for Paleoclimatology in the International Tree-Ring Data Bank in Boulder, Co. (Guyette 1996*b*) and are available for use.

Outside ring dates on the CWD were not the same as the date of tree death. No residual bark occurred on any of the logs that we sampled or observed, which might indicate that no annual rings were missing. However, the circuit uniformity of the outer rings, the smooth circular shape of the logs, and the presence of a nearly complete sapwood layer on many of the logs did indicate that very few were missing, especially from many of the more recently fallen CWD. The number of rings on each sample was not significantly correlated with their outer ring date (Table 2).

The outside ring date and each log's 1994 shoreline location are shown in Fig. 1. The majority (79%) of the CWD sampled was found in bays and shallow areas with gently sloping bottoms on the north and east shorelines. The south and west shorelines held 21% of the CWD sampled. Rocky points and littoral zones with steep slopes had fewer eastern white pine logs. Only 8% of the CWD that we sampled had remained where it had fallen into the lake. This was determined from the generally perpendicular orientation of the log to the shoreline and the portion of the log that was still on shore. The majority (92%) of the CWD sampled had drifted and changed position within the lake. This was evidenced by the positive buoyancy of the CWD and its parallel orientation to the shore in areas of CWD accumulation.

Some of the logs had residual large branches, but most of these branches were <1 m long. Since the most recently fallen CWD in our sample dated to some time before about 100 years ago, it appears that most limbs break off eastern white pine logs during the first 100–150 years in the water. Even the most recent additions of eastern white pine CWD had no bark, indicating that the degradation and removal of the bark takes less than a century.

Most of the littoral zone eastern white pine CWD was free of heart rot and had at least some solid wood that appeared free of decay and defect. More than 97% of our samples included some sound heartwood and the pith. About 44% of the CWD sampled was from upper sections of the tree bole having large branches and knots, while 56% was from bole sections without branches.

Many characteristics of the eastern white pine CWD were related to the age and residence time of the wood in the water. The average calendar year (mean of inner and outer rings, Fig. 2) for each of the 82 dated eastern white pine CWD samples (Table 1) was 1551, or 443 years old (1994–1551). The average date of the center ring on each sample was 1449. The length of eastern white pine CWD ranged from 1.5 to 26.5 m (Table 1) and was weakly correlated with the outside ring date of the CWD. The outside ring date of CWD was significantly correlated with the logarithm of CWD dry mass (Table 2). Variability in mass was much greater for logs that entered the lake during the past 300 years. Ring shake, tangential separations along adjacent ring boundaries, was negatively correlated with the outermost ring date (Table 2).

A significant correlation was found between outside ring dates and the percentage of the bole underwater (Table 2). Although the oldest logs were usually completely underwater, some younger CWD was completely submerged as well. Some CWD with outside rings dating back more than 500 years was still floating. Occasionally, the cut ends of a previously sunken log would float to the surface after being sampled.

We detected a slight decline in the specific gravity of the CWD through time from the significant correlation among outside ring dates and CWD specific gravity (Table 2) for wood that appeared free of decay and defect. A logarithmic transformation of specific gravity yielded no improvement in the correlation coefficient. Since we sampled large (CWD with enough rings to date) and well-preserved CWD, our specific gravity measurements are biased toward values that are higher than whole-log or whole-lake values. One sample of CWD that had been in the littoral zone for over 800 years was disintegrating into small pieces along the ring boundaries and had an average specific gravity of 0.29 g/cm^3. Cell wall thickness for this sample averaged 4.1 versus 6.7 µm for a recently fallen live eastern white pine.

The difference between maximum and minimum diameters of the CWD was correlated with its outside ring dates (Table 2). An example of the differential weathering and the maximum and minimum diameters of a cross section of CWD is shown in Fig. 3. A slight increase in the strength of correlation ($r = -0.60$, $p < 0.001$) for diameter differences

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Table 1. Statistics describing temporal and physical characteristics of eastern white pine CWD.

Variable	*n*	Minimum	Maximum	Mean	SD
Outer ring date (years)[a]	82	1147	1893	1661	182.2
Mean ring date (years)[b]	82	1039	1815	1551	180.9
Pith date (years)	82	930	1760	1449	186.1
Number of rings	82	86	406	212.1	69.5
Dry mass (kg)	51	13.5	1497.0	308.0	292.0
Specific gravity (g/mL)[c]	57	0.286	0.418	0.345	0.030
Maximum diameter (cm)	82	17.0	70.0	39.4	10.1
Minimum diameter (cm)	82	8.0	63.0	31.8	12.4
Length (m)	82	1.5	26.5	10.7	6.6
% submergence	78	30.0	100.0	70.5	23.7
Ring shake[d]	89	0	6	1.3	1.5

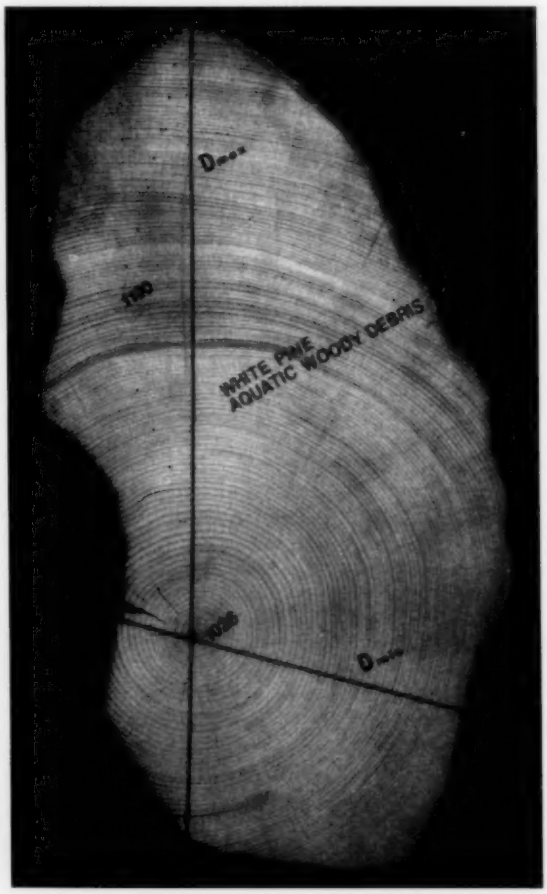
[a]Calendar year of outermost ring on the sample.
[b]Mean of the outer ring date and pith date.
[c]Oven-dry specific gravity of sound wood (appearing free from decay and defect).
[d]Number of separations along ring boundaries on the sample.

Table 2. Correlation coefficients between outside rings dates and physical characteristics of CWD illustrating the effects of time in the littoral zone on CWD.

CWD characteristic	*n*	*r*	*p*
Maximum diameter (D_{min}) (cm)	82	0.14	0.204
Minimum diameter (D_{max}) (cm)	82	0.34	<0.001
Diameter ratio (D_{max}/D_{min})	73	–0.53	<0.001
Diameter difference ($D_{max} - D_{min}$)	73	–0.49	<0.001
Diameter difference (>9 m) ($D_{max} - D_{min}$)[a]	31	–0.60	<0.001
Ring shake	89	–0.38	<0.001
No. of rings	82	0.13	0.231
Log length (m)	82	0.22	0.054
% submergence	77	–0.49	<0.001
Specific gravity (g/mL)[b]	57	0.36	<0.001
1/dry mass (kg)	53	0.48	0.006
Surface roughness[c]	82	0.36	<0.001

[a]Logarithm of diameter difference for a subset of logs >9 m in length.
[b]Oven-dry specific gravity of sound wood (appearing free from decay and defect).
[c]Two-class categorical variable (rough or smooth).

Fig. 3. Cross-sectional disk from the third oldest eastern white pine sample, dating from 1026 to 1184. Minimum diameter (D_{min}) and maximum diameter (D_{max}) are shown. This log had extensive weathering on three of its radii, resulting in a relatively large diameter ratio (D_{max}/D_{min} = 37 cm/16 cm = 2.31).



and outside ring dates is found for a subsample of CWD stratified by length (logs > 9 m). This stratification removes the effects of end weathering on diameter differences of short CWD. The natural logarithm of the difference (centimetres) in the maximum and minimum diameters ($D_{max} - D_{min}$) can be roughly estimated from the age (years BP) of the CWD by using the regression equation

$$\ln(D_{max} - D_{min}) = 0.91 + 0.0025(\text{age}).$$

Results from this equation predict the differences in maximum and minimum rates of surface decay to be about 0.3 mm/year. Thus, in about 1000 years, an eastern white pine log in the littoral zone of Swan Lake would lose at least 30 cm more from one of its surfaces than from another. The

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Fig. 4. Age of the CWD mass equal to or greater than a given date. A negative exponential curve (percent mass = $-6 + 106\ \exp^{-0.0030t}$, t = years BP) is fit to the percent mass of CWD and outside ring dates. Fifty percent of the eastern white pine mass in the littoral zone dated to more than 275 years BP. The outside ring dates, used as proxies for the date of tree death, are biased by wood loss toward more ancient dates by 30 years or more. No large eastern white pines have fallen in the water in the last 100 years.

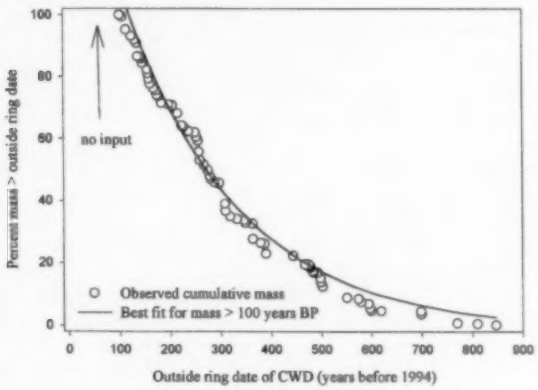
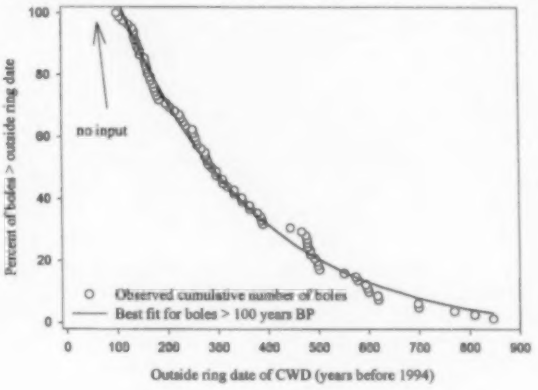

Percent mass > outside ring date
no input
Observed cumulative mass
Best fit for mass > 100 years BP
Outside ring date of CWD (years before 1994)

Fig. 5. Age of CWD abundance (number) equal to or greater than a given date. A negative exponential curve (percent boles = $-18 + 118\ \exp^{-0.0021t}$, t = years BP) is fit to the percentage of CWD and outside ring dates. Fifty percent of the number of eastern white pine CWD pieces had outside rings dating to more than 285 years BP. The outside ring dates, used as proxies for the date of tree death, are biased toward more ancient dates by 30 years or more.


Percent of boles > outside ring date
no input
Observed cumulative number of boles
Best fit for boles > 100 years BP
Outside ring date of CWD (years before 1994)

maximum rate of surface decay in the lake is greater than this differential rate of 0.3 mm/year.

An exponential decay function was fit to cumulative CWD mass as a function of outside ring age (Fig. 4). This descriptive equation (cumulative percent mass = $-1.24 + 174\ \exp^{-0.0045t}$) closely fits ($R^2$ = 0.99) the amount of eastern white pine mass and the frequency of CWD in the lake that date to a given period. Within limits (age > 100 years BP), this equation best describes the age of the CWD in Swan Lake. Also, the equation only describes littoral CWD. Deep-water CWD was not measured and could affect the age structure of all the CWD in the lake. Estimates from this equation indicate that about half of the CWD mass is from logs that have outside ring dates > 275 years BP.

The number of eastern white pine logs versus the outside ring age is an important measure of habitat in the lake littoral zone and is also described by a negative exponential function. An exponential decay function was fit to cumulative CWD frequency as a function of outside ring age (Fig. 5). This descriptive equation (cumulative percent boles = $-3.3 + 159\ \exp^{-0.0038t}$) closely fits ($R^2$ = 0.99) the number of boles in the lake that date to a given period. The descriptive value of this equation is also limited to littoral (not deep-water) CWD and to CWD with outside ring dates greater than 100 years BP. Estimates from this equation indicate that about half of the boles in the lake have outside ring dates > 285 years BP.

Discussion

There is an unknown degree of bias in using outside ring dates as proxies for the date of tree death. Since nearly every sample had an unknown number of rings eroded from its original outer surface, our estimates of the year of tree death (outside ring dates) from outer ring dates are biased toward more ancient calendar dates than the date of actual tree death. No significant correlation between the number of rings on each CWD sample was detected even after the data were transformed (reciprocal and logarithmic functions) and stratified by age periods. Since the number of rings contained on each sample was not significantly correlated with its outer ring date, we conclude that the selection of the radius with the most rings may have minimized the trend in weathering and loss of rings from the radius selected for dating and measurement. There remains, however, an overall bias in representing dates of tree death by outer ring dates. This bias is the difference between the average number of rings on a tree bole that falls in Swan Lake and the average number of rings on our sample sections. A subsample of 10 well-preserved (diameter ratio < 1.1) and recently dead (outer ring dates > 1830) logs with nearly intact sapwood had a mean age of 242 years. This 242-ring estimate is a reasonable estimate of the age of trees falling in the water in an old-growth forest. This subsample, although small, indicates that the overall sample mean (212 years, Table 1) might be missing about 30 rings (242–212). Here, we present the outer ring dates as proxies for the year of tree death with the strong reservation that there is a bias in the estimation of tree death dates that may be as great as 30 years or more. Relative to the length of the chronosequence of CWD dates that spans over eight centuries, this 30-year bias toward more ancient dates is small. We found no comparable studies on the age of CWD in lake littoral zones. Submergence in water is known to slow the rate of decay and weathering of wood (Hoffmann and Jones 1990) compared with the rate of decay in most natural terrestrial environments. Subfossil pines (*Pinus* spp.) from a lake in northern Finland (27°04′E, 69°54′N) date to more than 2000 years BP (Zetterberg et al. 1995). These pines, which grew well below the present lake level, were submerged by rising lake levels and recovered at depth by divers. Although the pines in this Finnish study are

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not comparable with littoral zone CWD in more temperate latitudes, they do illustrate the preservation of wood in lakes. As expected, studies on wood in mesic terrestrial environments indicate much shorter periods of decay. Tyrrell and Crow (1994) estimated that eastern hemlock CWD in northern Michigan and Wisconsin has a half-life of 33 years. Means et al. (1985) estimated the half-life of Douglas-fir (*Pseudotsuga menziesii*) terrestrial CWD at 98 years. Although considerable work has been done on the effects of CWD in streams, we found no study that determined the age of CWD in streams.

The long-term buoyancy and consequent drifting of eastern white pine have implications for the distribution of CWD in lakes. The location of 79% of the eastern white pine CWD on the east and north shores is consistent with CWD drifting forced by prevailing westerly winds. Since eastern white pine CWD may float for many centuries, it can create navigation problems for boats and aircraft long after the shoreline forest has been removed or changed in species composition. There may also be habitat implications that involve the uneven distribution of CWD around lakes caused by the accumulation of eastern white pine driftwood. Studies are being undertaken to determine the distributions of pine trees, the physical characteristics of the littoral zone CWD accumulation, and CWD movement in lakes (Hayes and Cole 1996).

The degree of submergence and the buoyancy of the CWD have habitat implications. Trees that are anchored at one end on the shoreline and with positive buoyancy, a condition of many recent tree falls into the lake, create habitat over deep water that is accessible from shore. The percentage of submersion was correlated with the length of CWD ($r = -0.40$, $p = 0.01$), indicating that longer logs stay afloat for greater periods of time. Floating logs can provide vertical structure, overhead cover for aquatic fauna, and "terrestrial" (above-water) structure and protection for plants, birds, insects, mammals, reptiles, and amphibians.

Many characteristics of the CWD samples were significantly but weakly correlated with their outside ring dates (Table 2). Initial conditions, as well as the effects of decay and erosion in the littoral environment, may account for much of the variability in these relationships. The initial characteristics of logs entering the water, such as length, diameter, wood density, terrestrial decay, and ring shake, probably add greatly to this variability. The higher variance among characteristics of CWD with more recent outside ring dates indicates that initial conditions are important. Differences between natural versus logging inputs of CWD to littoral zones may also have contributed to the variability of CWD characteristics in the more recent centuries.

We hypothesized that CWD would become shorter in length as it weathered in the littoral zone. This hypothesis was supported by the significant correlation between CWD length and residence time (Table 2). In contrast with what we expected, however, this relationship was very weak. Several factors may account for this. The initial length of the log may be highly variable depending on the distance of the tree from the water, the tree's direction of fall, and whether the bole breaks upon falling onto lake water or ice. Log length may have indirect habitat implications, since length may contribute to CWD buoyancy and structure in the littoral environment, such as extension into deeper water, attachment to the shoreline, and elevation over the lake bed substrate.

The correlation between outside ring dates and ring shake indicates that ring shake accelerates the decay rate of submerged eastern white pine. Ring shake allows the direct and rapid penetration of lake water and effectively increases the surface area of the log. Lake water can penetrate the wood much more readily via mass flow than through cellular diffusion. This exposes much more of the surface area of the CWD to oxygen and bacteria and other decay-enhancing organisms. Thus, ring shake can greatly enhance decay and shorten the residence time of CWD as habitat in littoral zones.

Differential weathering around the bole of CWD through time decreases circuit uniformity (deviations from a perfect circle). This hypothesis is supported by significant correlations among CWD residence times and the ratio (or difference by subtraction) of the maximum and minimum diameters of the cross sections (Table 2). Differential weathering is one of the few age-rated characteristics that could be used as a predictor of the relative age of CWD in lake littoral zones. Since few trees enter the lake with great differences in maximum and minimum diameters, the relationship is free of much of the variability due to the initial conditions and strong enough to have some predictive value.

The diameter difference and surface roughness of CWD have potential habitat implications. The surface of CWD weathers with age in the littoral zone from smooth and round boles to boles with cavities and depressions. Surface cavities and depressions may provide a refuge from predation for aquatic fauna as circuit uniformity decreases over time. In addition, the subjective classification of smaller and more regular deviations from circuit uniformity of the CWD surface was correlated with the outside ring date (Table 2). The surface condition of CWD and its habitat implications should be characterized in more detail in future studies.

Specific gravity of wood may have implications for macroinvertebrate populations that inhabit the outer decayed surfaces of CWD. For example, thousands of invertebrates per square metre (Bowden et al. 1995) may colonize near the surface of CWD but not the interior. The degraded and low-density wood on the outer surface (1–3 mm) of CWD has many small-diameter (1 mm) macroinvertebrate galleries. In addition, the positioning of these galleries longitudinally along the log and in the early wood of the annual ring indicates a preference by macroinvertebrates for low-density wood.

The mean calendar date of all the annual rings in the dated CWD was 1551, or 443 BP (1994–1551). This period is nearly four centuries long even with a 30-year bias in outside ring dates. This period is the average period from carbon assimilation in the living tree to the release of the carbon from the log in the littoral zone. The mean pith date (Table 1) of the CWD was 1449. Considering that most of the pith dates were taken from the upper boles and crowns of the trees, probably 50 years after the trees germinated on the forest floor, the actual mean date of germination is about 1400. Thus, eastern white pine CWD in the littoral zone of Swan Lake is from forest trees that, on the average, germi-

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nated about 600 years ago. Both these periods indicate that at least some components of terrestrial and aquatic ecosystems such as carbon budgets, habitat, and energy are coupled at very long periods with respect to the lives of most organisms in the littoral and nearshore environment. For example, hundreds of generations of invertebrates or young-of-year fish might utilize a single piece of CWD.

Between 1893 and 1995, no eastern white pine CWD appears to have entered the lake. This finding is consistent with the extensive and thorough late nineteenth century logging of the Swan Lake ecosystem for eastern white pine. The only eastern white pine trees left standing along the shoreline were very young unmerchantable trees, which have had a relatively low probability of windthrow or natural mortality over the past 100 years. Today, there are many eastern white pines up to 120 years in age along the shoreline of Swan Lake.

An unknown amount of CWD from logging in the late nineteenth century makes up much of the recent part of our data. We believe that a number of logs that we sampled resulted from logging rather than natural mortality, even though they showed no evidence of saw cuts or ax marks. The steep slopes of the curves (Figs. 4 and 5) between 100 and 200 years BP are evidence of the accelerated input of CWD in the late nineteenth century. Input pulses in the cumulative plot, such as the one that occurred circa 500 years BP (Fig. 5), are characterized by a steep slope of many dates followed by a gentle slope with few dates. The steep slope of the recent portion of the curve (Fig. 5) will become more apparent when trees start entering Swan Lake in the near future. Even the addition of one new data point now (Fig. 5, year 0) will define a curve with a very gentle slope over the last 100 years that abruptly changes to a steep slope coincident with the period of eastern white pine logging (100–200 years BP). Alternatively, part of the steep slope of the curve could be due to exponential changes in depletion rates.

The effects of logging on the abundance and temporal distribution of CWD are open to many interpretations. If the eastern white pine had not been cut, continued input of CWD over the last century and the addition of tree boles that were taken out of the ecosystem could have resulted in more CWD than we now observe in the lake. The removal of many of the tree boles from the ecosystem could have had a significant and overall effect on littoral CWD mass that could go undetected. On the other hand, if the eastern white pine around Swan Lake had not been logged, some of this woody debris (especially that from younger trees) would still be present as living trees along the shoreline and not have contributed to CWD input.

Exponential decay is a reasonable model to explain the rate of CWD degradation in a lake littoral zone and has been used to describe wood decay (Harmon et al. 1986). Negative exponential functions have been used to describe other natural systems and decay processes, such as radioactive isotope loss (Faure 1977) and the decline of tree-ring widths with age (Fritts 1976). More research is needed, however, to determine the relationships among the physical, chemical, and biotic factors in lakes and CWD age and structure. However, the information presented in Figs. 4 and 5 could be used to develop general decay functions as well as future age and stocking structure guidelines for the restoration and sustainable management of brook trout habitat in littoral zones.

Several resource management issues arise from the results and implications of this study. CWD should be viewed by resource professionals and the public as a dynamic and ancient component of the aquatic habitat of lake systems with input and depletion rates, rather than as a static structural component of lakes. A change in the perception of the age of CWD might translate into a change in value of CWD to the public.

Prohibitions on terrestrial ecotone logging and on CWD input to the aquatic system might be changed under certain circumstances. For example, CWD might be placed into the littoral zone of a lake to mitigate the effects of reduced CWD input rates due to shoreline development or logging. Alternatively, where logging debris has accumulated in lakes in excess of natural inputs, CWD might be allowed to be decrease over time. Research is needed to accurately estimate CWD input and depletion rates by tree species and types of forest–lake sites. A better understanding of relationships among CWD characteristics and fish productivity is needed.

The development of species composition in the forest–lake ecotones presents a management opportunity to influence littoral CWD. The differences between the specific habitat value of eastern white pine CWD and the CWD of other species are not know. Management recommendations could be made for the proportions of tree species in the shoreline ecotone based on the type of littoral habitat needed. The present diversity of tree species should be considered in terms of the future diversity of aquatic habitat.

Another management issue to consider is the potential for floating eastern white pine logs to become a navigation hazard to boats and floatplanes. If eastern white pine CWD is added to a lake to improve aquatic habitat, the logs should be secured to the bottom or to the shoreline in some way to keep them in their planned location. Caution should be exercised when eastern white pine CWD is disturbed during shoreline construction or other alterations. On lakes with heavy floatplane traffic, shoreline forests could be limited to tree species that are less mobile as CWD in lakes.

Conclusions

Studies of CWD can provide a valuable perspective on this important habitat in forest–lake ecotones. Although large CWD may appear to be ephemeral and transient, it is actually an ancient woody structure built up over as many as 10 centuries. White pine boles reside in the lake littoral zone for many centuries and have provided habitat for hundreds of generations of fauna from amphibious vertebrates to macroinvertebrates.

Tree ring dating can be used to estimate the age and time-related characteristics of CWD in littoral habitats. The average date of carbon fixation in eastern white pine CWD was 1551, or 443 years ago, while 50% of the eastern white pine boles were from trees that died over 275 years ago. No eastern white pine CWD habitat has been created in the littoral zone over the last 100 years due to the complete logging of larger eastern white pine during the late 1800's. The temporal age structure of CWD mass and abundance can be characterized by negative exponential decay functions. This age

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structure is the result of both input rates and decay rates. The observed characteristics of CWD were highly variable through time, especially for recent additions of CWD. Many CWD characteristics that may effect littoral habitat such as mass, length, diameter differences, specific gravity, and percent submergence were significantly correlated with the outside ring dates of CWD.

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Recent declines in the recreational catch of coho salmon (*Oncorhynchus kisutch*) in the Strait of Georgia are related to climate

R.J. Beamish, G.A. McFarlane, and R.E. Thomson

Abstract: Wild and hatchery-reared coho salmon (*Oncorhynchus kisutch*) from streams and rivers that flow into the Strait of Georgia are caught in the Strait of Georgia and off the west coast of Vancouver Island. The percentage of coho caught in either of these two areas varies from year to year. The variation is associated with the flow of freshwater from the Fraser River and became more extreme in the 1990's. In four of eight years in the 1990's and in the past three years, most coho have been caught outside the Strait of Georgia. The dramatic decline in the sport catch in the Strait is related to ocean conditions in the Strait. The change in ocean conditions is related to an increase in the number of days of zonal (westerly) winds in October, November, and December and to an increase in relative sea level height. The climate change about 1989 that affected the pattern of winter winds and the circulation in the Strait of Georgia was associated with changes in other global climate indices, demonstrating the impact that global climate events can have on the dynamics of regional salmon stocks.

Résumé : Des saumons cohos (*Oncorhynchus kisutch*) sauvages ou élevés en pisciculture provenant de cours d'eau se jetant dans le détroit de Georgia sont capturé chaque année dans le détroit et au large de la côte ouest de l'île de Vancouver. Le pourcentage de cohos capturés dans ces deux secteurs varie cependant d'une année à l'autre. Cette variation, qui est liée au volume d'eau douce provenant du Fraser, s'est accentuée au cours des années 90. Durant quatre des huit années écoulées durant cette période, et au cours des trois dernières années, la plupart des saumons cohos ont été capturés à l'extérieur du détroit de Georgia. La baisse inquiétante du nombre de prises sportives dans le détroit est liée aux conditions océaniques qui y règnent. Le changement de conditions océaniques est imputable à une augmentation du nombre de jours avec vents zonaux (de l'ouest) en octobre, novembre et décembre, ainsi qu'à une élévation relative du niveau marin. Le changement climatique qui, vers 1989, a modifié le régime des vents en hiver et la circulation dans le détroit de Georgia a également provoqué des changements intéressant d'autres indices climatiques. Cela démontre à quel point les événements climatiques d'envergure planétaire peuvent influer sur la dynamique des stocks de cohos à l'échelle régionale.

[Traduit par la Rédaction]

Introduction

The coho salmon (*Oncorhynchus kisutch*) fishery in the Strait of Georgia (Fig. 1), on the west coast of Canada, was one of the most important sport fisheries in Canada. In 1994 the recreational fishery for coho throughout British Columbia was estimated to be worth $295.3 million in Canadian currency (Gislason et al. 1996). In the Strait of Georgia, it accounted for $218.5 million (74%), even though 1994 was a poor year for total coho catches (Fig. 2). In the 1990's, many coho in their first ocean year left the Strait of Georgia and did not return the following year during the normal fishing period. From 1980 to 1990 the recreational fishery for coho in the Strait of Georgia caught an average of 508 000 individuals annually, with a range of 288 000 – 1 003 000. In 1991, 1995, 1996, and 1997, the years of extreme movement offshore, the average annual catch was 26 000, with a range of 5000 – 46 000. Although they were accessible to the commercial and recreational fishery off the west coast of Vancouver Island, the value of coho to the recreational fishery was substantially less, as most sportfishing occurs in the Strait of Georgia. Here, we show that a change in climate is associated with the change in behaviour that caused the recent collapse in the sport fishery for coho in the Strait of Georgia.

In general, coho spawn in coastal rivers and streams in the late fall and die after spawning (Sandercock 1991). The fry remain in the river over winter and go to sea in the spring of the following year. In this paper, we refer to these juveniles as ocean age 0, or their first year in the ocean. These fish suffer very high ocean mortality and the few survivors feed in the ocean until they reach a size the following year that allows them to be retained by the fishery. We refer to these fish as ocean age 1, but other methods of identifying age are also used (Sandercock 1991). Most coho caught in the oceans fisheries are ocean age 1, but they can be identified as 1.1 (1 freshwater year and 1 marine year). It is the ocean

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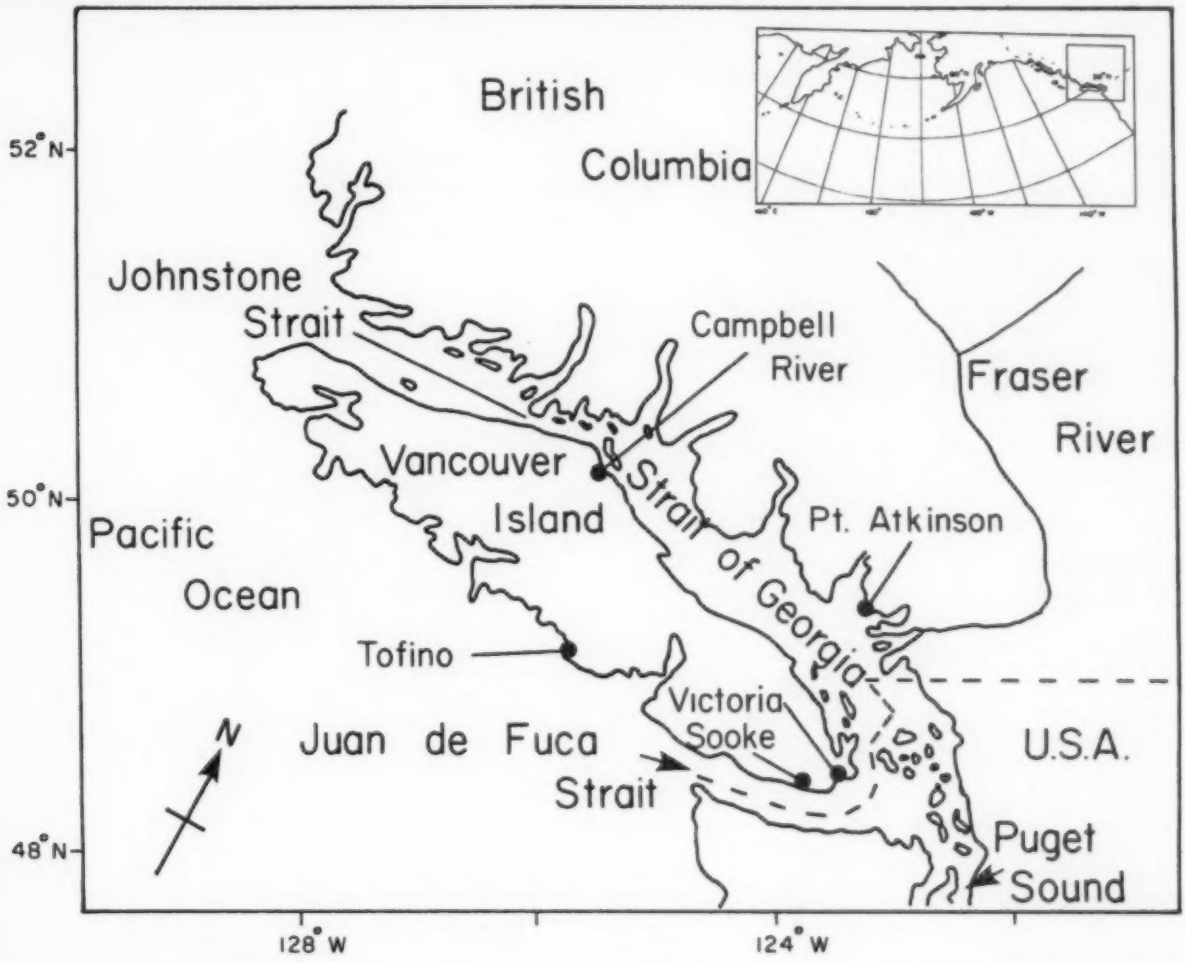
Fig. 1. Study area with insert showing the location of Vancouver Island in the North Pacific Ocean. The broken line is the border between Canada (British Columbia) and the United States.



age 1 coho that survive the fisheries that provide the spawning escapement to the rivers in the late fall.

Methods

Estimates of percentage of coho offshore

Estimates of the percentage of coho that enter the Strait of Georgia and are caught on the west coast of Vancouver Island exist since 1976 (Simpson et al. 1997). These estimates were for the three largest hatcheries (Quinsam River, Chilliwack River, Big Qualicum River) and represent an average 58% of the hatchery production in the 1990's. We also estimated the percentages of coho caught off the west coast that were produced in all hatcheries that released their production into the Strait of Georgia. Coho caught off the west coast of Vancouver Island (or in the Strait of Georgia) could originate from a number of stocks both in Canada and in the United States. Because a small percentage of most hatchery coho are tagged, it is possible to identify the portion of the catch that originates from the Strait of Georgia stocks. These estimates of coho that moved out of the Strait were considered to be close approximations, even though effort and the time of year of capture were not considered. The percentages were calculated using coded-wire tagged (CWT) coho released from hatcheries. The number of coho from each hatchery was determined by expanding the estimated catch of coho with CWT's according to the percentage marked by each hatchery. The percentages of hatchery fish contributing to the catch inside and outside the Strait of Georgia were then determined. The percentages were used to represent the movement of wild and hatchery fish. It is the behaviour of the hatchery fish, however, that we are studying as indicated by the proportion of CWT reported in the two areas. The behaviour of the hatchery fish appears to be similar to that of wild fish, as the pattern of reported total catches of hatchery and wild coho is similar to the pattern of movement of hatchery fish (Fig. 2). The percentage of hatchery coho in the catches of Strait of Georgia stocks increased. In 1997, it was estimated that 76.6% of the juvenile coho in September in the Strait of Georgia were from hatcheries (Beamish et al. 1998). Prior to 1995, coho catches in the Strait of Georgia and off the west coast of Vancouver Island were not actively managed (Department of Fisheries and Oceans 1996). The sport fishery for coho remained open all year in both areas and there were no changes in the management of the commercial fishery from 1985 to 1993 that would have an impact on the relocation of

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effort from one area to the other. Exploitation rates remained high (65–80%) and the number of coho returning to spawn generally declined (Rice et al. 1995; Department of Fisheries and Oceans 1996). Thus the percentage of hatchery coho in the catch in the two areas is representative of abundance in the areas. Active management started in 1995, but the sport fishery in the Strait of Georgia had already collapsed (Fig. 2).

Survey methods

Coho were captured from 1995 to 1997 using a large rope trawl (described in Beamish and Folkes 1998). Sets were made throughout the Strait of Georgia from 06:00 to 18:00 at depths ranging from the top 15 m to >100 m. As few coho were caught below 45 m, most of the fishing effort was in the top 45 m. A comprehensive survey of the Strait of Georgia could be completed in less than 10 days. These surveys were undertaken in the spring shortly after coho entered the ocean and in the summer, fall, and winter. We report the results of some of these surveys to establish the timing of movement out of the Strait of Georgia in 1996–1997.

Creel census

Sport catch and effort have been monitored in a creel census program since 1980 and reported in a series of publications (Collicutt and Shardlow 1995). The presence of coho in the Strait of Georgia during the winter in past years was examined using these reports of sport catches. Unfortunately the reports were produced sporadically, but they are the only available assessment of coho presence in the Strait of Georgia in the winter.

Winter wind types off the west coast of British Columbia

A classification of the westerly winds was made for October–March from 1972 to 1996 using the procedures of McKendry (1994) and Yarnal (1993). We used a correlation-based map pattern classification method to examine synoptic-scale circulation for each day (October–March) off the west coast of Canada for the years 1972–1996. The fields were derived from the Canadian Meteorological Centre gridded sea surface pressure data set for the Northern Hemisphere by synthesizing the fields covering the region from northern Washington to northern British Columbia. The Kirchofer technique is an approach to synoptic classification in which map patterns are normalized to remove the seasonal cycle and are placed into discrete categories on the basis of an interactive procedure that compares all grids by a sums of squares measure (Yarnal 1993). Daily direction of winds off British Columbia from 1976 to the fall of 1996 were categorized into 17 types. These types were similar to the 26 types reported in Moore and McKendry (1996). In this study, we report only the days of zonal winds (directly towards Vancouver Island and Juan de Fuca Strait). The other dominant types are meridional flows from the north or from the south.

Sea level heights, salinity, and temperature

Sea level heights were derived from hourly coastal tide gauge records archived by the Marine Environmental Data Services (Ottawa, Ont.) and the Canadian Hydrographic Services (Sidney, B.C.). These data have been carefully edited to remove erroneous values and to correct offsets associated with recording format (e.g., feet versus metres), missing records, data retrieval software, and repositioning of gauges. The edited sea level heights were used to generate hourly time series of sea surface differences between selected pairs of gauge stations. Since exact geodetic elevations of the tide gauges are not known (i.e., the gauge positions have not been accurately surveyed), the measured sea level differences are not representative of the true sea level slopes between the stations. To circumvent this problem, we first portioned the difference records by month and calculated the global averages (mean monthly values) for each of the 12 months using all available data in that record. This yields the annual cycle in monthly mean sea level difference, which serves as a reference for further analysis. Months having fewer than two complete tidal cycles (25 h) were omitted from the averaging process. We then calculated the time series of monthly average values for each difference series and subtracted the mean monthly values (mean annual cycle) for that station pair. This gives the monthly anomaly of sea level difference relative to the long-term mean for each pair of stations. Positive values indicate that the monthly sea level gradient between the pair of stations increased relative to the average gradient, while negative values indicate that the monthly gradient decreased. Sea surface salinity and temperature data taken at lighthouses in the Strait of Georgia (including Chrome Island) were accessed through the Institute of Ocean Sciences website http://www.ios.bc.ca/ios/osap/data/lighthouse/bcsop.htm. A relationship between coho movement out of the Strait of Georgia and sea surface salinity in the Strait in February has been identified in unpublished reports (i.e., Simpson et al. (1997).

Results

Offshore migration and relationship with surface salinity and temperatures

Except for the years 1991, 1995, 1996, and 1997, the fluctuations in catch of hatchery fish outside the Strait of Georgia compared with inside ranged from about 20% to about 60% (Fig. 2A). In 1991, 1995, 1996, and 1997, few coho were caught in the sport or commercial fisheries in the Strait of Georgia, confirming that few wild or hatchery coho were in the Strait (Fig. 2B). The sport catches in the Strait of Georgia for 1991, 1995, and 1996 averaged only 6% of the average catches from 1980 to 1990 (Fig. 2B). The 1997 data are preliminary, and are lower for the Strait than in 1996. There is a distinct, inverse relationship between the catches in the Strait of Georgia (Fig. 2B) and the proportion of hatchery fish caught offshore (Fig. 2A). The fluctuations in catch/movement became extreme in the 1990's and there was evidence of reduced movement offshore in 1993 that corresponds to a high catch in the Strait of Georgia. Because the percentage of hatchery fish caught offshore determined from all hatchery releases and the three largest hatcheries was virtually identical, we used the estimates from all hatchery releases in the comparisons with physical parameters.

In the late 1980's, there was an earlier start in the spring of increasing Fraser River discharge. Because the Fraser River receives most of its water from snowmelt in the mountains, the lowest flows occur in the winter and the highest in June. Even though the annual mean flow has declined since 1976 (Beamish et al. 1995), more water has been flowing out of the Fraser River earlier in the year in the 1990's (Fig. 3B). A comparison of the anomaly of the percentage of all hatchery produced coho caught offshore with either the anomaly of the annual Fraser River flow (Fig. 3A) or the anomaly of the winter (December–March) Fraser River flow (Fig. 3B) shows that there is a similarity in the patterns. In years, or winters, of high flows, a higher percentage of coho are caught offshore. The relationship is better when the winter flows are used ($R^2 = 0.27$, $P = 0.07$ compared with an $R^2 = 0.07$, $P = 0.38$ for the annual anomaly 1976–1988). Beginning about 1991, the general pattern of higher Fraser River flow and more coho movement offshore remains, but the impact of

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Fig. 2. (A) Percentage of hatchery coho that enter the Strait of Georgia that are caught outside the Strait of Georgia or "offshore". The broken line (triangles) represnts the percentage catch from the three largest hatcheries and the solid line (squares) is for all hatcheries. (B) Number of coho caught in the sport (crosses) and sport and commercial (squares) fisheries in the Strait of Georgia. The 1997 value is preliminary.

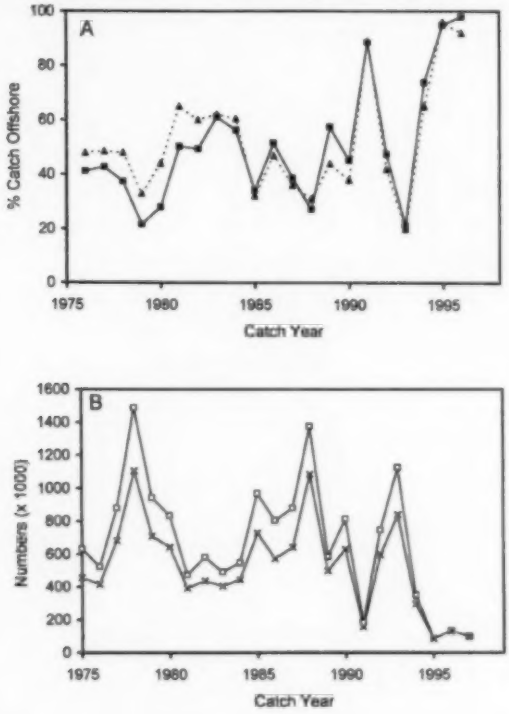
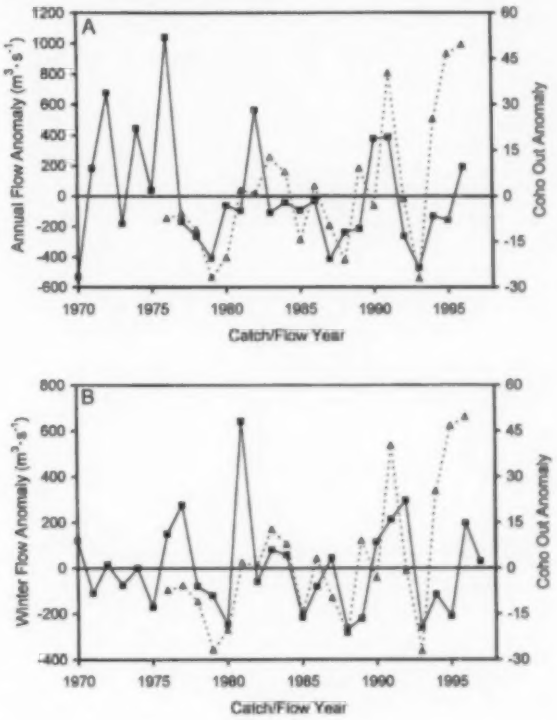


Fig. 3. (A) Annual flow from the Fraser River from April 1 to March 31 (flow year; this flow year is used because flows are lowest at this time) expressed as an anomaly from 1970 to 1996 (solid line, squares) compared with the anomaly of the offshore catch of coho from all Strait of Georgia hatcheries (broken line, triangles). (B) Relationship as in Fig. 3A, but for Fraser River winter flows (December–March).



higher or increasing flows is greater, suggesting that something in the relationship changed in the 1990's.

Sea surface salinity in the Strait of Georgia is inversely related to Fraser River flows in winter (Fig. 4A), and particularly in February (Fig. 4B). A regression analysis of the February Fraser River flow anomalies with the February Chrome Island salinity anomalies for the 1976–1988 and 1976–1997 periods identified significant ($P < 0.05$) inverse relationships ($R^2 = 0.38$ and $R^2 = 0.25$, respectively). This sea surface salinity relationship with Fraser River flow in the southern Strait also changes beginning in the early 1990's (Fig. 5A). A regression analysis shows a close relationship between the surface salinity in February and the offshore catch of all hatchery-produced coho in the same year ($R^2 = 0.60$, $P < 0.01$) (Fig. 5B). The salinity anomaly is largest in February (Fig. 5A), but both the 6-month period from October to March and the 3-month period from December to February have similar distinct shifts in their relationship with river flows in the 1990's. The years 1990 and 1993 were periods of higher salinity in the Strait and years when either an average or a large percentage of coho did not move to offshore waters.

The sea surface temperature (SST) anomaly patterns for winter (December–March) in the Strait of Georgia did not correspond closely to the pattern of catch offshore (Figs. 6A and 6B). The combined temperature from all lighthouse sites (Fig. 6A) and the Nanoose site (Fig. 6B) (for a history of the Nanoose site, see Beamish et al. 1995) had similar anomaly patterns, confirming that both temperature series were similar. In 1991, 1995, 1996, and 1997 when coho abundance was high offshore, two years had above-average winter SST in the Strait of Georgia and two were below average. In 1993, the winter SST anomaly was similar to 1995, yet in 1993, few coho were caught offshore, and in 1995, large numbers were found offshore. Also, there was a very poor relationship between Fraser River flow and SST in the Strait ($P > 0.4$). Offshore, at Amphitrite Point (Fig. 6C), the years of high offshore abundance of coho were years of slightly above-average SST, yet the extreme values in 1992 did not result in extreme movement offshore.

Sea level heights

Sea levels were shown as monthly anomalies of sea level difference between selected stations (Fig. 7). Campbell River, in the northern part of the Strait of Georgia (Fig. 7), was compared with Victoria at the eastern end of Juan de Fuca Strait. Campbell River also was compared with Pt. Atkinson in the southeastern portion of the Strait of Georgia. Pt.

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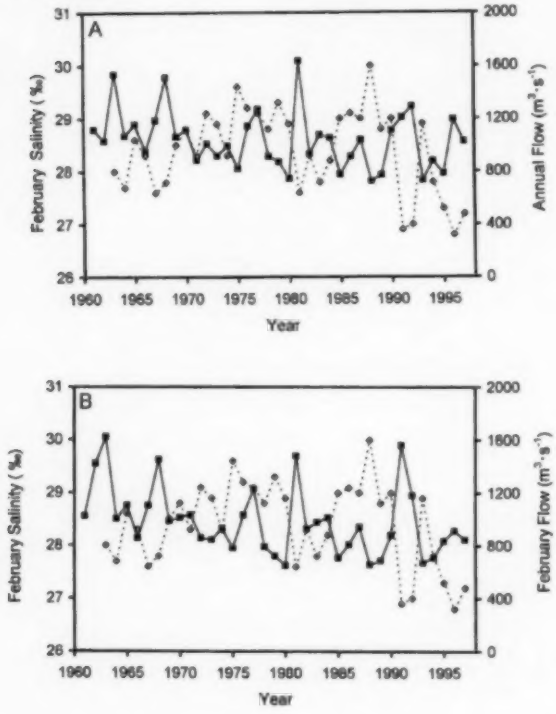
Fig. 4. (A) Average sea surface salinity at Chrome Island lighthouse in February (broken line, diamonds) compared with the average annual Fraser River flow (April 1 – March 31) (solid line, squares). (B) Relationship as in Fig. 4A, but for February flows.

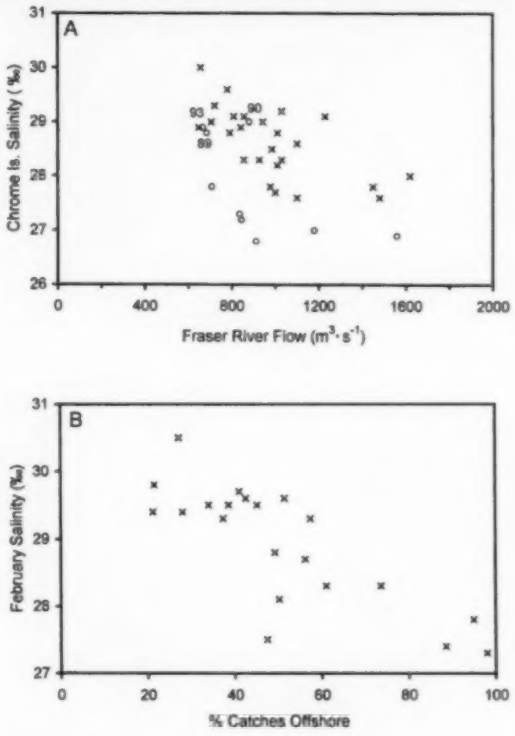


Atkinson and Victoria were compared with Tofino, on the Pacific Ocean side of Vancouver Island.

Beginning in 1989, there was an abrupt change in sea level gradient within the coastal waters, with relatively higher sea level heights at Victoria compared with Campbell River. There was an equally abrupt increase in sea level at Pt. Atkinson compared with Campbell River, and both Victoria and Pt. Atkinson had higher sea levels relative to Tofino (several other stands of relatively high water between these two regions are found in the records, but these have short time scales compared with the protracted change in 1989). The change in sea level height between inside the Strait of Georgia and the offshore areas (specifically, Tofino) was more abrupt for Pt. Atkinson than for Victoria.

The sea level differences show that there was an abrupt increase in relative sea level beginning in 1989 at the eastern end of Juan de Fuca Strait (Victoria). This increase was associated with an equally abrupt increase in relative sea level in the southern Strait of Georgia compared with the northern end of the strait (Pt. Atkinson versus Campbell River). The 1991–1992 El Niño event in the Pacific Ocean affected the sea level difference between Victoria and Campbell River, and there was a short-term reduction in sea level difference in 1993 between Pt. Atkinson and other sites (specifically, Campbell River and Tofino) that corresponds to the reduced coho movement offshore (Fig. 2A). However, these were all short-term events compared with the persistent change in relative sea level that began in 1989.

Fig. 5. (A) Average February surface salinity in the Strait of Georgia at the Chrome Island lighthouse compared with the total monthly Fraser River flows in February. Crosses indicate values from 1963 to 1988; circles indicate values from 1989 to 1997. It is clear that the relationship changes in the 1990's. Note that in 1993 the salinity is higher and the coho catches in the Strait of Georgia were also large. (B) Relationship between surface salinity in February and the percentage of coho caught offshore.



Winter winds

The number of days of offshore zonal winds (Fig. 8, insert) was summed for October, November, and December and shown as the average total number of days per month for the three months (Fig. 8). The highest number of days of offshore zonal winds for this period occurred after 1989 (Fig. 8). The high percentages of coho offshore in 1991, 1995, and 1996 (Fig. 2A) were associated with a higher number of days of zonal winds in the previous winter. The relationship is not exact, as the low number of days in 1993 did not result in extremely high catches in the Strait of Georgia in 1994, indicating that factors in addition to wind direction may be involved in the salinity changes. A more detailed analysis that weights direction with speed may explain the inconsistencies, but the relationship as presented shows that the change in the pattern of winds in the 1990's was associated with the physical oceanographic changes in the Strait of Georgia.

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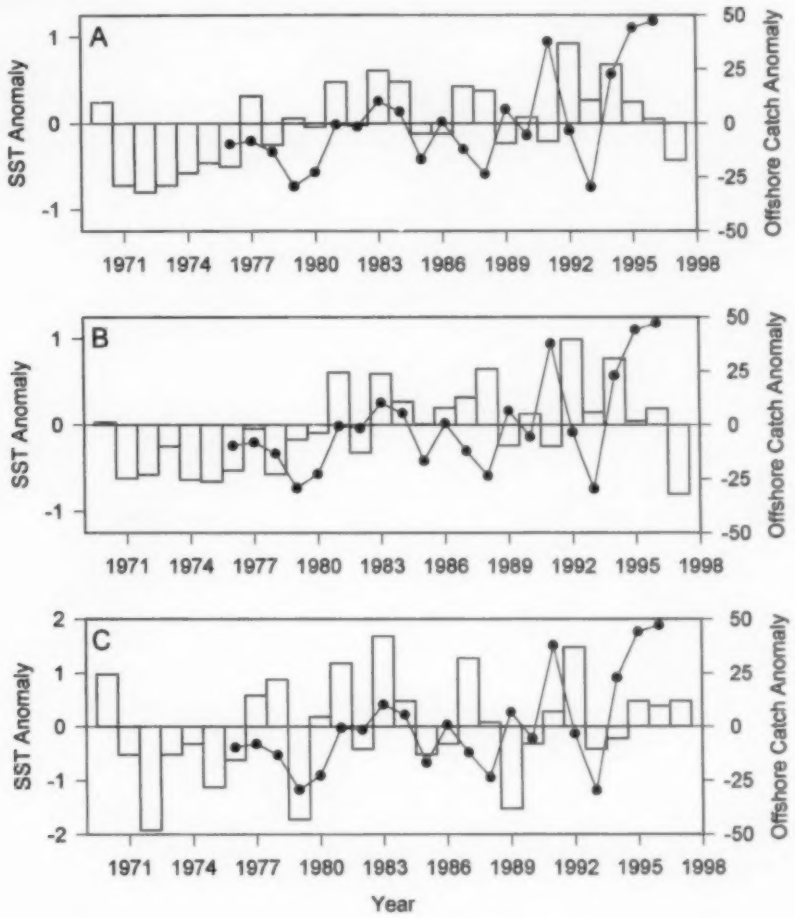
Fig. 6. Sea surface temperature (SST) anomaly for December–March for (A) the combined lighthouse data and (B) the temperatures from the Nanoose site reported in Beamish et al. (1995). (C) SST anomaly for the offshore site (on the west coast of Vancouver Island) at Amphitrite Point. The solid line in each panel is the percentage of hatchery fish caught offshore that were released from all Strait of Georgia hatcheries.



Juvenile coho surveys

In September 1996, 164 tows were made throughout the Strait of Georgia (Table 1). The standardized catches (catch per hour) indicated that coho were slightly more abundant in the north than in the south (Table 1). In November 1996, the 42 tows caught fewer coho throughout the Strait of Georgia, particularly in the north (Table 1). In February 1997 and March 1997, no coho were caught in the 34 tows in the Strait of Georgia (Table 1).

Creel surveys

The results are listed as catch per "boat-day", which is the catch per boat for 1 day of fishing. There was variation in the interview effort among years, and in some years, there were no interviews in the winter. The data for January and February were combined because catches and effort were low. Even though the data were considered minimal, the number of boat days surveyed was quite large (Table 2). In years when the outside catch was exceptionally high (1991, 1995, 1996), there was no evidence that coho were present in either the north or south in the winter. In years when catches were high in the Strait of Georgia (1988, 1993), the winter catches were relatively high.

Discussion

The 21-year history of catches of coho that enter the Strait of Georgia as smolts in one year shows that a varying percentage of these fish are caught outside the Strait of Georgia in the next year. The pattern of this variation of catch inside and outside the Strait of Georgia is similar to the proportion of hatchery coho caught in these areas and can be divided into two distinct periods on the basis of the extreme behaviour that occurred in the 1990's. Moreover, this recent change in behaviour matches known changes in climate that are both global and regional.

Fraser River flow was associated with the percentage of catch outside the Strait of Georgia, and the relationship

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Fig. 7. Sea level height anomalies for various locations around the Strait of Georgia and offshore (on the west coast of Vancouver Island). Sea level heights are expressed as differences in anomaly values between locations, and all show an abrupt change in the 1990's.

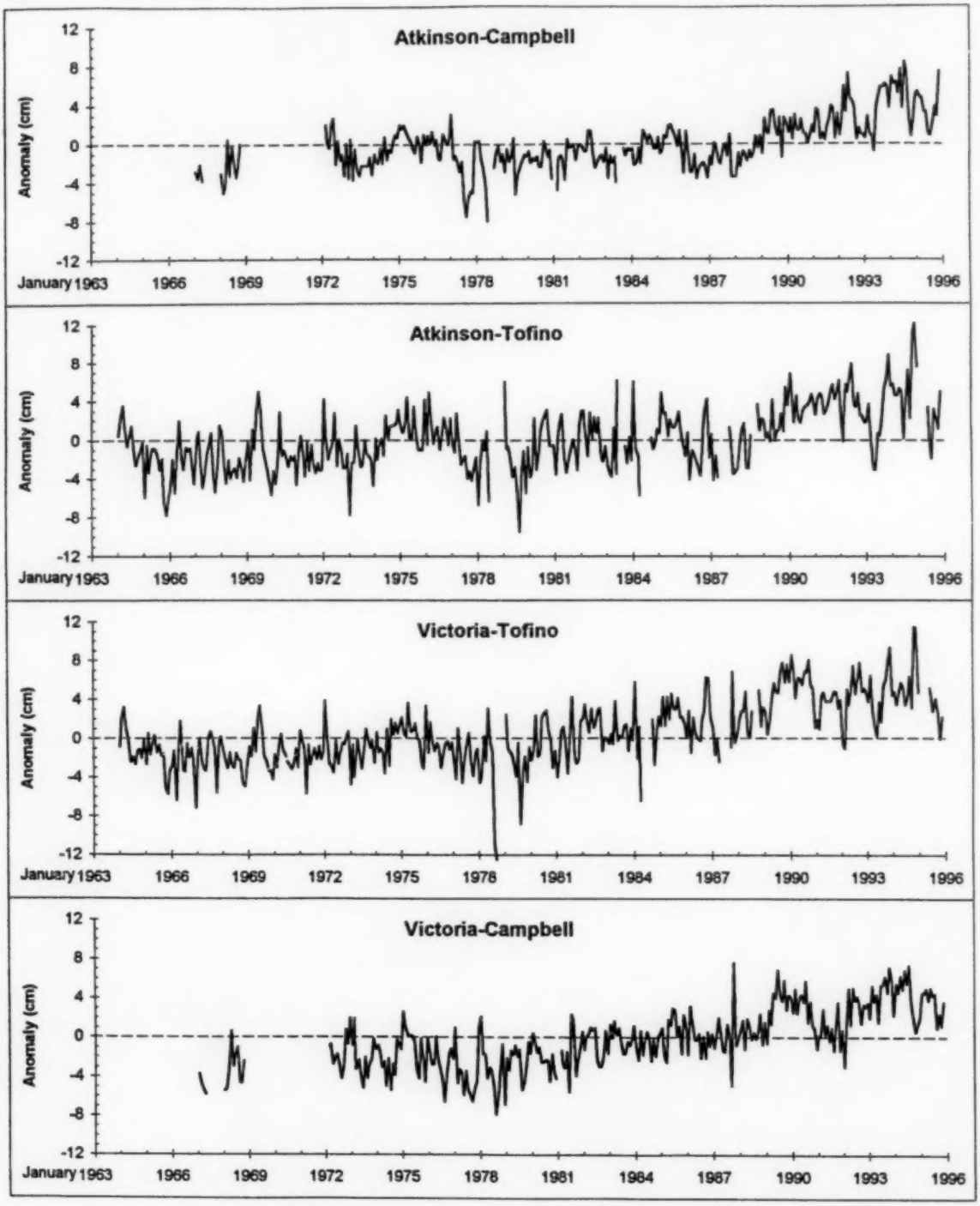

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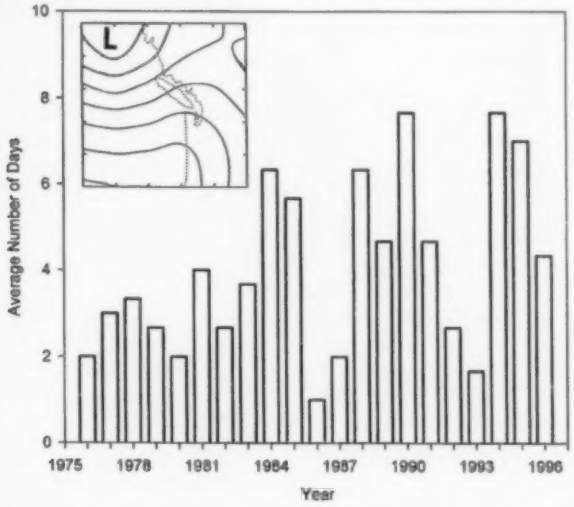
Fig. 8. Number of days of the most typical zonal wind pattern averaged for the 3-month period October–December. The insert shows the typical zonal flow pattern (L is the area of low pressure).



changed in the 1990's. The February salinity and Fraser River flow comparison clearly showed a shift in the response. Beamish et al. (1997*a*, 1997*b*) proposed that there was a shift in the climate in the Pacific Ocean about 1989. Indicators of global climate such as the Southern Oscillation index and the Aleutian Low Pressure index changed about the late 1980's. Trenberth and Hoar (1996) also found that the climate pattern in the tropical Pacific in the early 1990's was unique in this century. One change that is relevant to the behaviour of coho was a change in the dominant direction of the westerly winds in the winter. The dominance of westerly winds in the winter after about 1989 probably increased the frequency of estuarine circulation reversals, or at least reduced the strength of the near-surface outflows. The estuarine circulation results from the outward flow of Fraser River freshwater through Juan de Fuca Strait and the compensatory flow of nutrient-rich bottom water into the Strait. In the winter, the circulation can be reversed if strong westerly (zonal) winds increase the sea level height at the western extremity of Juan de Fuca Strait. Perhaps the best evidence for a reduced outflow of brackish water from the Strait of Georgia in the 1990's, and therefore reduced overall salinity in the Strait, is the abrupt increase in sea level slope between the Pt. Atkinson tide gauge and gauges outside the Strait. The question is whether the magnitude of the sea level change (roughly about 3–5 cm) is reasonable given the area of the Strait of Georgia and the mean volume runoff from the Fraser River. Using a typical average runoff of 3000 $m^3 \cdot s^{-1}$ and the known surface area of 6800 km^3 for the Strait of Georgia (Thomson 1981), the time-rate-of-change of sea level due to runoff is (3000 $m^3 \cdot s^{-1}$)/6800 km^3 = 4.4 × 10^{-7} $m \cdot s^{-1}$ (assuming all of the runoff is spread over the surface of the basin). If we assume that the enhanced westerly winds during the 1990's caused an effective 1-day delay in the flushing of brackish water to the ocean during the entire winter period of 3 months (about a 1% increase in the winter flushing time), the net change in sea level is 4.4 × 10^{-7} m × c × 0.864 × 10^5, where c = 3.8 cm, which is consistent with the observed increase in sea level difference. In other words, a small change in the retention time of water in the Strait of Georgia could account for the change in sea level slope and associated change in upper layer salinity. The earlier onset of the spring freshet as seen in the higher winter flows may exacerbate this effect. Thus, the more frequent westerly winds blowing directly across the Pacific contribute to more frequent reversals and a lowering of the salinity in the southern Strait of Georgia. The change in wind pattern may also explain why the onset of the annual Fraser River freshet is occurring earlier. However, it is not possible to explain all aspects of the mechanisms responsible for the abrupt lowering of the surface salinity in the Strait of Georgia in the 1990's. For example, the role of rainfall remains difficult to assess.

In 1996, we were able to show that coho smolts that entered the Strait of Georgia from freshwater were distributed throughout the Strait until the fall. By fall, there was both a change in the overall catch rates in the north and south of the Strait and a decline in catch rates in the north compared with the south. This indicated that coho were migrating south and apparently out of the Strait of Georgia. In February and March of the following year, there were virtually no coho in

Table 1. Catch per hour of ocean age 0 coho in the Strait of Georgia in 1996 and ocean age 1 (the same brood year) in 1997.

	North	South
September 1996	111 (15)	53 (37)
November 1996	9 (16)	22 (26)
February and March 1997	0 (13)	0 (21)

Note: The number of tows is given in parentheses. Depth range is 0–45 m. The north and south areas were determined by drawing a line approximately across the middle of the Strait of Georgia.

Table 2. Coho catch per boat-day in the sport fishery in the Strait of Georgia.

	January–February		March	
	North	South	North	South
1981[a]	0.4 (700)	0.1 (4400)	0.2 (500)	0.4 (2800)
1982	—	—	—	—
1983	0.2 (1101)	0.1 (1040)	0.7 (751)	0.4 (1932)
1984	1.3 (646)	0.1 (1757)	2.8 (474)	0.7 (1894)
1985	1.0 (446)	0.05 (917)	2.6 (645)	0.3 (1814)
1986	0.1 (443)	0.1 (2138)	2.5 (993)	2.0 (1883)
1987	0.4 (1094)	0.3 (2774)	0.7 (405)	0.5 (1802)
1988	5.1 (1213)	0.4 (2278)	3.8 (870)	1.8 2672)
1989	0.6 (629)	0.3 (1695)	1.6 (1139)	0.6 (1894)
1990	1.8 (399)	0.4 (992)	2.3 (1303)	0.7 (2168)
1991	0.1 (275)	0(905)	0 (417)	0 (1120)
1992	1.7 (475)	1.0 (691)	1.2 (1097)	2.0 (3490)
1993	0 (580)	4.3 (1463)	1.8 (272)	5.2 (1000)
1994	0 (514)	0.1 (944)	0.3 (500)	0.8 (1271)
1995	—	—	(144)	(422)

Note: The number of boat-days is given in paremtheses. The north is Statistical Area 14 and the south is Statistical Area 17. A dash indicates that no surveys were made. No surveys were made in 1996.

[a]Data were not collected until May.

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the Strait of Georgia. There was no question that coho left the Strait of Georgia late in the first ocean year and were virtually absent by February of the second ocean year in 1997.

We cannot determine if a late-fall southern migration, possibly out of the Strait, is normal behaviour or is a consequence of the present conditions in the ocean ecosystem. In the 1980's and early 1990's, coho were captured in the sport fishery in the winter, but the relative abundance was unknown except that the extreme low and high estimates in the creel census match the sport catch record for the rest of the year. We interpreted the creel census data to indicate that in the past, some coho did not leave the Strait in the winter. Off Oregon and Washington, juvenile coho were observed to migrate seasonally with a north migration in August and September (Pearcy and Fisher 1988). Thus, it would not appear unusual that coho in the Strait of Georgia had a seasonal migration pattern. Movement completely out of the Strait, however, is unusual. The response of coho to ocean conditions and climate identified in this study indicated that the movement of coho may be profoundly affected by ocean conditions. This response contrasts with reports that there were specific migratory and nonmigratory types of coho in the Strait of Georgia (Milne 1950; Healey 1978) If such types did exist, our study would indicate that climate and ocean conditions probably influenced the general behaviour of coho in the 1950's. If distinct migratory and nonmigratory types still exist, they were equally affected by the ocean conditions in the 1990's.

Beamish et al. (1994) identified a relationship between the annual volume of water flowing out of the Fraser River and the relative survival of coho. In general, total coho survival (the total catch and escapement compared with juvenile production) was always average or above average in a year when the annual flows declined from a high level in the previous year to a low level. Conversely, when flows increased from a low level to a high level, the survival was either poor or average and never above average. The relationship was believed to be associated with changes in the salinity of the surface layer (St. John et al. 1992; Beamish et al. 1994), although the mechanism was not determined. In this study, it was the increased flow in the winter and the annual flow that were related to movement out of the Strait of Georgia. Reduced surface salinity in the winter was also associated with offshore movement as shown here and in earlier studies (i.e., Simpson et al. (1997). However, our fishery surveys indicated that most coho left the Strait of Georgia before February; thus, February salinity levels are an indicator of earlier ocean changes that influenced the behaviour of coho. The change in climate about 1989 changed the relationship between Fraser River flow and surface salinity such that surface salinities were lower for similar levels of flow before and after 1989 (except around 1993 when wind patterns changed and relative sea levels dropped). If the reduced survival reported by Beamish et al. (1994) was more related to reduced surface salinity than higher flow, the changes in the 1990's may also result in reduced survival.

Why coho move out in their first ocean year when the surface salinity is low and do not move back into the Strait of Georgia in their second ocean year is not known. Coho may prefer colder, saltier water in the winter, so there may be a physiological basis for leaving. There also may be a relationship with the availability of preferred food items or even an avoidance of a competitor. Once coho leave, it appears that most coho stay out of the Strait of Georgia almost until it is time to return to their respective spawning streams and rivers.

Despite our inability to understand all of the details of the mechanisms that affected the movement of coho, there is little doubt that the recent behaviour change in coho is related to a change in climate. We are not proposing that the movement out of the Strait is exclusively related to physical changes in the ocean, but rather that there is a clear impact of climate. It is important to emphasize that a relationship among coho migration, Fraser River flows, and salinity existed from the 1980's to the 1990's, but the impacts changed when the pattern of atmospheric circulation changed. A signal of climate impacts on the behaviour of coho focuses our attention on the role of climate in fisheries management. It also reminds us that we need to pay attention to the message that global climate change is occurring (Kerr 1995).

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PERSPECTIVE

The regime concept and natural trends in the production of Pacific salmon

R.J. Beamish, D.J. Noakes, G.A. McFarlane, L. Klyashtorin, V.V. Ivanov, and V. Kurashov

Abstract: Large fluctuations in the trends of Pacific salmon production in this century have been linked to trends in climate in the Pacific that are in turn associated with climate trends throughout the Northern Hemisphere. The close correspondence in the persistence of climate trends and the synchrony of the changes is evidence that a common event may cause the regime shifts. The trends or regimes can be characterized by stable means in physical data series or multiyear periods of linked recruitment patterns in fish populations. The regime concept is important in fisheries management because the natural shifts in abundance may be large and sudden, requiring that these natural impacts be distinguished from fishing effects. An equally important consideration is that biological and physical mechanisms may change when regimes shift, resulting in conditions that may not be characterized in the earlier part of the data series. Fluctuations in Pacific salmon abundance in this century were synchronous with large fluctuations in Japanese sardine abundance, which can be traced back to the early 1600's. The synchrony in the fluctuations suggests that Pacific salmon abundance may have fluctuated for centuries in response to trends in climate. The concept of regimes and regime shifts stresses the need to improve our understanding of the mechanisms that regulate the dynamics of fish and their ecosystems.

Résumé : Les amples fluctuations observées dans les tendances de la production de saumon du Pacifique au cours de ce siècle ont été liées à des tendances du climat dans le Pacifique, elles-mêmes associées aux tendances climatiques de l'ensemble de l'hémisphère nord. L'étroite concordance de la persistance des tendances climatiques et la synchronie des changements montre à l'évidence qu'un événement commun peut causer les changements de régimes. Les tendances ou régimes peuvent être caractérisées par des moyennes stables dans les séries de données physiques ou par des patrons liés de recrutement dans les populations de poissons sur des périodes de plusieurs années. Le concept de régime est important en gestion des pêches car les changements naturels dans l'abondance peuvent être forts et soudains, et qu'il est donc nécessaire de distinguer ces impacts naturels des effets de la pêche. Autre aspect également important, les mécanismes biologiques et physiques peuvent changer quand les régimes se modifient, ce qui crée des conditions qui n'étaient pas forcément caractérisées dans la partie précédente de la série de données. Les fluctuations de l'abondance de saumon du Pacifique au cours de ce siècle étaient synchrones des grandes fluctuations de l'abondance de la sardine japonaise, qu'on peut faire remonter jusqu'au début du 17^{e} siècle. Cette synchronie permet de penser que l'abondance de saumon du Pacifique fluctue peut-être depuis des siècles en fonction des tendances climatiques. Le concept de régime et de changement de régime fait ressortir la nécessité de mieux connaître les mécanismes qui régissent la dynamique des poissons et de leurs écosystèmes.

[Traduit par la Rédaction]

Introduction

There is increasing evidence of persistent patterns and synchronous changes in the climate/ocean environment in the Pacific Ocean (Venrick et al. 1987; Ebbesmeyer et al. 1991; Latif and Barnet 1994; Polovina et al. 1995; Roemmich and McGowan 1995; Ware 1995; Gargett 1997; Gu and Philander 1997; Mantua et al. 1997). Evidence is also accumulating to show that large-scale trends in Pacific salmon abundance are linked to trends in climate. In recent years, a series of studies have identified both large-scale and regional linkages (Beamish and Bouillion 1993; Francis and

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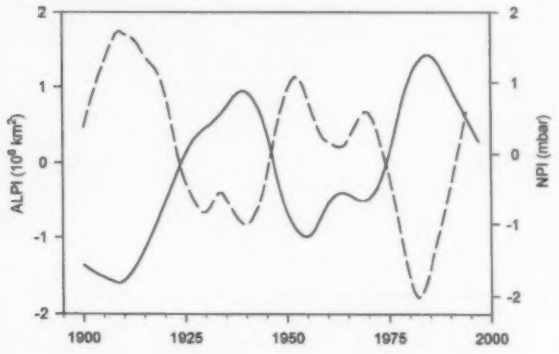
Fig. 1. Loess (f = 0.2) smoothed relationship between the Aleutian Low Pressure index (ALPI) (solid line) (Beamish et al. 1997*a*) and the North Pacific index (NPI, 1 mbar = 100 Pa) (broken line) (Trenberth and Hurrell 1995) (website http://www.cgd.vcar.edu/cas/clmind/np.html). The inverse relationship results from the use of pressure measurements for NPI and area of low pressure for ALPI. As the area of low pressure gets larger, the estimate of average low pressure becomes smaller.



Hare 1994; Hare and Francis 1995; Adkinson et al. 1996; Beamish et al. 1997*a*; Mantua et al. 1997; Pearcy 1997). As the linkages are with climate, the impacts are seen over an aggregate of stocks and not necessarily at the individual stock level. The fluctuations in Pacific salmon abundance have been shown to correspond to shifts in macrozooplankton abundance (Brodeur and Ware 1992; Sugimoto and Tadokora 1997) that can be linked to physical changes in the ocean (Lagerloef 1995; Polovina et al. 1995). The trends in salmon abundance are not necessarily the same for all areas of the ocean, as climate shifts can also cause large-scale oscillations in ocean productivity (Gargett 1997) with regional impacts (Adkinson et al. 1996). The release of large numbers of juvenile salmon from hatcheries provides convincing evidence that reduced total abundance in some areas was a result of ocean conditions and not of a reduction in the production of juveniles (Beamish et al. 1995; Pearcy 1997). Also, in areas of the subarctic Pacific where large increases in salmon abundance occurred, the rate of increase among species appears unrelated to the number of juveniles produced in hatcheries, suggesting a strong influence of ocean conditions on the abundance trends (Beamish et al. 1997*b*).

Direct measures of productivity are difficult, but Adkinson et al. (1996) demonstrated that an abrupt shift in the productivity parameter of the standard Ricker curve could model the shifts in abundance of Bristol Bay sockeye salmon (*Oncorhynchus nerka*) stocks. Although Adkinson et al. (1996) did not identify shifts in the productivity parameter of sockeye salmon from the Fraser River, Beamish et al. (1997*a*) did detect a shift that was synchronous with the 1976–1977 climate shift. Furthermore, they showed that after 1977 the total returns of sockeye salmon from the best-studied population in the river increased up to two times for the years of largest smolt production.

These persistent trends in the dynamics of fish populations or in climate/ocean conditions can be termed "regimes" (Namias 1953; Graham 1994; Steele 1996), which we define as a multiyear period of linked recruitment patterns in fish populations or as stable means in physical data series. A regime shift is a synchronous change in these variables. An important question is whether the trends in Pacific salmon abundance have always shifted naturally. If natural trends occur, then fisheries management should account for this phenomenon when assessing the impacts of fishing and developing management strategies. The possibility that Pacific salmon populations fluctuate naturally is an important competing hypothesis to the concept that abundance is regulated solely by fishing and an intrinsic population relationship that are relatively independent of the environment or associated species.

In this study, we examine six indices of climate over the Northern Hemisphere for persistence and for synchrony of change. We combine four of these indices to produce a regime index. We relate these indices of global climate to Pacific salmon production and to historical information on Pacific sardine (*Sardinops* spp.) catches to show that salmon populations may have undergone shifts in production in association with climate for centuries. We use the total catches (Canada, United States, Japan, and Russia) of pink (*Oncorhynchus gorbuscha*), chum (*Oncorhynchus keta*), and sockeye salmon to represent the total production of Pacific salmon, as the catches of these species account for about 90% of the total catch of all salmon species (Beamish and Bouillon 1993). Catch of Pacific salmon has been used as an estimate of production (Beamish and Bouillon 1993; Hare and Francis 1995; Mantua et al. 1997) because exploitation rates are high, ranging from about 40 to 80%. We do not use the index of Pacific climate oscillations developed by Mantua et al. (1997), but we do compare it with the indices used in our study.

Climate indices

Aleutian Low Pressure index and North Pacific index

Beamish and Bouillon (1993) used an Aleutian Low Pressure index (ALPI) as an indicator of a major climate process that could affect Pacific salmon production. Trenberth and Hurrell (1995) used another index of the Aleutian Low Pressure system, the North Pacific index (NPI), which is virtually the inverse (Fig. 1, r = –0.86) of the ALPI described in Beamish et al. (1997*a*). In Fig. 1, we show the smoothed (loess f = 0.2) ALPI plotted against the smoothed (loess f = 0.2) anomaly of NPI. Trenberth (1990) showed that the NPI is closely associated with the Northern Hemisphere teleconnection pattern of Wallace and Gutzler (1981), establishing a linkage with midtropospheric wind patterns. Both the ALPI and NPI are suitable indices of the winter climate in the subarctic Pacific. In this study, we use the ALPI.

The Aleutian Low is the winter weather pattern over the North Pacific Ocean that strengthens late in the year and weakens in the spring of the following year. The varying levels of low pressures affect the intensity of winter storms, which affect both midocean and coastal productivity (Venrick et al. 1987; Gargett 1997) through changes in the horizontal and vertical flows. We determined the index from 1899 to show the long-term pattern in the trends but compare the ALPI with other indices beginning in 1950, as the sea level pressure data are most reliable after this date (Tren-

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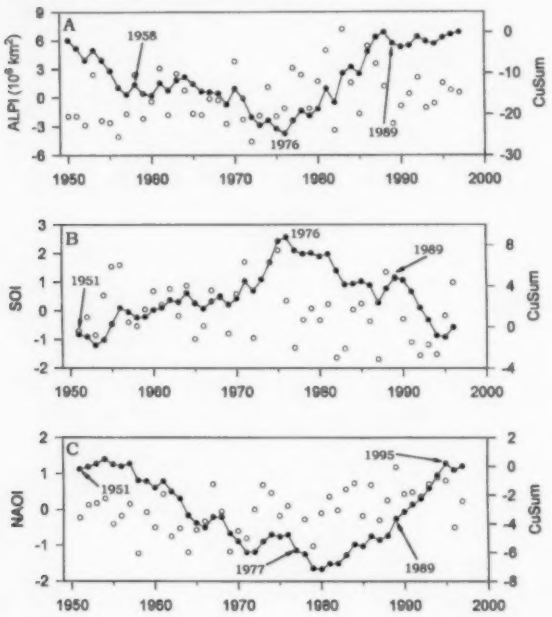
Fig. 2. Anomaly values (open circles) and CuSum's (solid circles) of three pressure indices. (A) Aleutian Low Pressure index (ALPI) from 1950 to 1997 and the CuSum showing distinct trends during 1950–1976, 1977–1989, and 1990–1997. (B) Southern Oscillation index (SOI) from 1951 to 1996. The extreme negative anomalies are El Niño events and the extreme positive anomalies are La Niña events. There are changes in 1989 and 1996, but they do not affect the general slope of the graph from 1977 to 1996. (C) North Atlantic Oscillation index (NAOI) from 1951 to 1997 showing the change to positive anomalies in the 1980's and the CuSum showing distinct trends during 1951–1980 and 1981–1995.



berth and Hurrell 1995). The cumulative sum of the anomalies was estimated to provide a simple visual picture of the trends in the index. The method of accumulating sums or CuSum (Murdock 1979) is a way of studying trends by including information from past data points and giving less weight to single values. The calculation is a simple addition of a datum point to the sum of all previous data points. Each datum point may have a constant subtracted from it to enhance visualization of trends in the series. The constant is usually the mean of the entire series. If there is a trend in the data, there will be a trend in the CuSum graph. A positive slope indicates an above-average or increasing trend and a negative slope represents a below-average or decreasing trend. The year of the change in the slope of the CuSum is the year that a regime shifts.

The ALPI (Fig. 2A) shows a trend of higher pressures (smaller areas of low pressure and a corresponding smaller index) from 1950 to 1976. There is a brief period from 1958 to 1963 where moderately intense winter pressures occurred, but the general pattern was one of reduced areas of intense low pressures. The ALPI identifies a period of extreme low pressures from about 1977 to 1988 (Fig. 2A) and average pressures after 1988. The CuSum graph (Fig. 2A) shows the general trend of reduced low pressures up to 1976 and a change in slope that reflects the increased areas of intense low pressures up to 1988. The weaker lows beginning in 1989 appear as a change in slope of the CuSum and a trend toward average conditions.

The various indices employed in this paper were examined using standard statistical and time series analysis techniques (Box and Jenkins 1976). These procedures have been employed to analyze data in a number of fields of study including fisheries (e.g., Stocker and Noakes 1988; Campbell et al. 1991; Noakes and Campbell 1992) and readers are referred to the literature for details of these models and techniques. An intervention analysis (Noakes 1986; Hipel and McLeod 1994) was used to study the timing and significance of the changes in the ALPI anomaly time series from 1950 to 1997. The analysis uses the time series to test for significant shifts at selected years. Both the 1977 and the 1989 changes in the ALPI anomaly time series were significant ($P < 0.05$).

Southern Oscillation index

The Southern Oscillation index (SOI) is the difference in sea level pressures between Darwin (Australia) and Tahiti. The oscillation of air masses in the tropical Pacific between the western and eastern Pacific oceans was first described by Walker (1924). The index is formed by subtracting the mean sea level pressure from the annual or monthly averages and dividing by the standard deviation. The SOI used in this study is the standardized series of the standardized Tahiti data minus the standardized Darwin data. When the index is negative, the sea level pressure gradient across the tropical Pacific is in an El Niño or warm state, and when it is positive, it is in the La Niña or cool state. The linkage between the Southern Oscillation and El Niño or El Niño – Southern Oscillation (ENSO) was recognized in the late 1960's (Bjerkness 1969). An El Niño event occurs when the sea level pressures at Darwin are anomalously high, resulting in a series of atmospheric–ocean shifts that have global teleconnections (Trenberth and Shea 1987). Thus, the atmospheric–ocean shifts in the tropical Pacific are of global importance. The La Niña event may be more restrictive in its impacts, affecting the eastern North Pacific (Cayan and Webb 1992), and its impacts are not the opposite of El Niño (Hoerling et al. 1997). La Niña is a state that receives very little recognition in comparison with an El Niño and particularly with respect to the impacts on fish populations.

The SOI that we show extends from 1951 to the end of 1996 and is the average annual value (Fig. 2B). The index has the familiar oscillations between El Niño (negative) and La Niña (positive) states, but there are also three distinct patterns. The regime up to 1977–1978 is characterized by the well-known quasibiennial cycle (Reed et al. 1961; Veryard and Eldon 1961) where there is an oscillation between El Niño and La Niña events. Beginning in 1977, there is a succession of El Niño events without the extreme La Niña events. This pattern changes again in 1988–1989 with a strong La Niña. The period in the 1990's is characterized by even more intense El Niño like conditions (Trenberth and Hoar 1996) as a consequence of persistent high sea level pressures in the western Pacific and at Darwin. The CuSum graph (Fig. 2B) identifies a trend from 1951 to 1976 and

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from 1977 to 1987. There is a change in trend in the data from 1988 to 1989 and in 1990, but the slope of the graph does not change substantially after 1990, indicating that the trend to extreme high pressures over Darwin persisted. An intervention analysis of the standardized anomalies from 1951 to 1996 identified a significant ($P < 0.05$) change in 1977 but not in 1989–1990.

North Atlantic Oscillation index

The North Atlantic Oscillation index (NAOI) is the difference between the normalized winter (December–March) sea level pressures at Lisbon, Portugal, and Stykkisholmar, Iceland (van Loon and Rogers 1978). The North Atlantic Oscillation is a well-known climate pattern associated with alternating high winter temperatures and low pressures (and vice versa) between a number of centers. The phenomenon has been known for centuries, but was formally described by Walker and Bliss (1932) and recently by van Loon and Rogers (1978) and Barnston and Livezey (1987). Strong positive anomalies occur in the northwestern Atlantic Ocean when the Icelandic low is intense as a result of strong westerly winds flowing from the north over western Greenland. Negative anomalies occur with a weakening of the westerly winds and reduction in the intensities of the Icelandic Low. The oscillations are associated with changes in the intensity and position of dominant wind patterns, which also affect precipitation and temperature patterns (Walker and Bliss 1932; van Loon and Rogers 1978; Hurrell 1995). The relationship also forms a teleconnection with other areas (van Loon and Rogers 1978). There is a relationship between the intensity of the Icelandic Low and the Aleutian Low in the Pacific (Walker and Bliss 1932; Wallace and Gutzler 1981), confirming the global nature of the indices.

Our data are the standardized series of the standardized sea level pressure anomalies at Lisbon minus the standardized sea level pressures at Iceland. Other formulations of the index exist (i.e., Hurrell 1995) and the trends are similar for the various formulations. The anomaly pattern (Fig. 2C) has a trend from negative values in the early part of the time series to positive values in recent years. There is a change in trend after 1979, a change in the anomaly pattern after 1989, which appears as a prolonged positive trend, and a major change in the index in 1996 to an extreme negative value. The CuSum chart (Fig. 2C) shows a distinct change in trend occurring about 1980 but no change in 1989. An intervention analysis of the NAOI from 1951 to 1997 identified a significant ($P < 0.05$) shift in 1981.

Atmospheric circulation in the Northern Hemisphere

We use the classification system developed by Russian meteorologists (Girs 1971; Barry and Perry 1973) to study the decadal-scale trends in the general circulation of the winds in extratropical regions of the Northern Hemisphere. The Russian system restricts the classification of wind patterns to three types. One type, the western (W) circulation, describes winds that follow a zonal pattern (latitudinal) without prominent meridional (north and south) circulation. The W circulation is typified by relatively fast east to west transfers of air masses. The meridional (C) flows have dominant northwest and southeast patterns that form weak subpolar lows but a strong high over Siberia. The easterly (E) circulation (also meridional) is similar in form to C but opposite in phase, resulting in different locations of the high and low pressure systems. The E circulation is also characterized by more intense lows, a weaker Siberian high, and a westward movement of the anticyclone areas in the Pacific and around the Azores. The C and E types result in northwest and southeast transfers of arctic and tropical air masses, as well as the establishment of large, quasi-stationary centers of atmospheric pressure over some areas.

As the Russian literature may be difficult to locate, we suggest that readers refer to the recent paper of Moore and McKendry (1996) or to Rodianov (1994). Moore and McKendry (1996) used a computer-assisted map typing process (Yarnal 1984, 1993) to classify the dominant direction of the westerly winds flowing over British Columbia, Canada, for the November–March period. We examined samples of the classifications made by the Russian specialists and Moore and McKendry (1996) and found that the classifications of the basic three types were similar. It is important to note that the actual classifications will depend on the size of the area studied. The dominant annual pattern of wind in small areas may be different from that in very large areas; thus the classifications are only directly comparable when similar areas are studied for similar periods.

In the Russian classification system, the proportions of days of each type were compared with long-term averages. An index of these patterns, the atmospheric circulation index (ACI), is developed from the anomalies for each pattern type. As the anomalies will add to zero, the index $C = -(W + E)$. The ACI is the integral or the sum of the W + E anomalies or the –C anomalies. The integral is a cumulative sum of the anomalies described earlier. Changes in the ACI have been linked to changes in trends of atmospheric pressure, temperature, and precipitation (Girs 1971) as well as to changes in the rotation of the solid earth or length of day (Sidorenkov and Svirenko 1991), which will be considered in a following section. Although our study compares indices beginning in 1950, the ACI starts in 1891. The ACI (Fig. 3A) indicates distinct trends during 1891–1902, 1903–1939, 1940–1972, and 1973–1990. A recent change started in 1990. As the ACI is a CuSum, we do not show a separate CuSum graph for the time series starting in 1950. An intervention analysis was conducted to examine changes in the ACI between 1950 and 1996. Trends in the series were removed using first differencing and the remaining autocorrelation structure in the data was identified and modeled appropriately. Significant ($P < 0.05$) changes in the ACI were detected in 1972 and 1991.

Northern Hemisphere land and ocean temperatures

The Northern Hemisphere surface temperatures (NHST) is a combined land and sea surface temperature series that we obtained from the databases at the Institute of Ocean Sciences, in Sidney, British Columbia. These data and earlier data published by Jones (1988) are also available from the Hadley Centre for Climate Prediction and Research, U.K., and the Climatic Research Unit, University of East Anglia, U.K. Warming that started at the turn of the century ended in the early 1940's, with a brief cooling period in the 1960's to the early 1970's. Since the mid-1970's there has again been a steady warming trend. The CuSum graph from 1950 to

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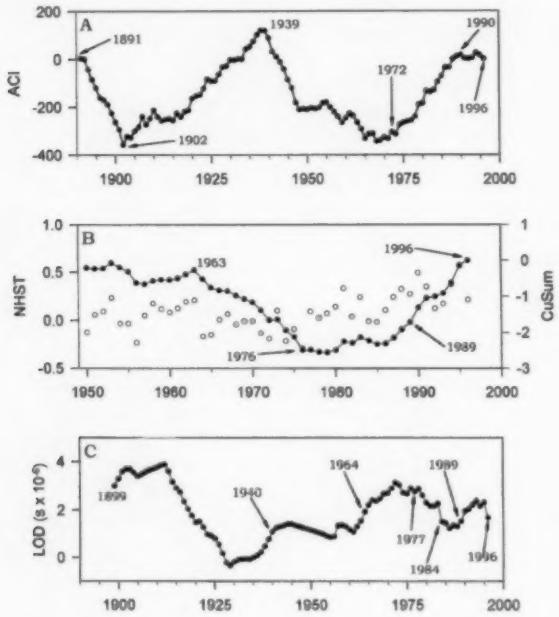
Fig. 3. (A) Index of general atmospheric circulation (ACI) from 1891 to 1996 showing the distinct fluctuations in trends. (B) Annual anomalies (open circles) of Northern Hemisphere surface temperatures (NHST) from 1950 to 1996 and the CuSum showing distinct trends during 1950–1976 that correspond to a modest cooling trend and during 1977–1996, which was a period of general warming. The period from 1977 to 1996 is seen as two trends that change to a more rapid warming period beginning about 1988. (C) Length of day (LOD) from 1899 to 1996.



1996 (Fig. 3B) shows changes in trends in the early 1960's, 1977, and mid-1980's. An intervention analysis of the anomaly series from 1950 to 1996 did not identify a significant ($P < 0.05$) shift in the time series in 1977.

Length of day

An index of environmental change that has been largely overlooked is an index of Earth rotation or the length of day (LOD). There is an extensive literature that documents the relationship between Earth rotational changes or angular momentum changes and climate. Here, we provide a brief review as well as show how the decadal-scale trends are consistent with trends in other climate indices.

The shells or the liquid core of the earth, the crust and mantle, the hydrosphere, and the atmosphere do not move at a constant rate (Munk and Macdonald 1960; Lambeck 1980; Barnes et al. 1983; Hide and Dickey 1991). Additionally, because of the principle of the conservation of angular momentum, there is a redistribution of angular momentum within the shells of the earth that can be seen as seasonal, interannual, and decadal trends in the measured LOD (Stephenson and Morrison 1995). The LOD is the difference between the astronomically determined duration of the day or universal time 1 (UT1) and the atomic clock time (TA1), which was established as exactly 86 400 s on January 1, 1958 (i.e., UT1 – TA1 = 0 on January 1, 1958). Changes in the LOD are expressed as the difference in the measured LOD relative to the standard LOD. Because the LOD is a derived value, there are minor differences in the time series used by various authors (Stephenson and Morrison 1984; McCarthy and Babcock 1986; Jordi et al. 1994). The data on the rotation of the earth that we use are from the International Earth Rotation Service in Paris, France (International Earth Rotation Service 1996, 1997). We identified a persistent trend in the LOD as the interval between the year in which a new trend started, extending through any periods of average trend up to the next change.

Table 1. Periods of increasing and decreasing length of day (LOD) from 1630 to 1995.

Increasing LOD	No. of years	Decreasing LOD	No. of years
1988–1995	8	1973–1987	15
1935–1972	38	1918–1934	17
1893–1917	24	1859–1892	32
1834–1858	25	1816–1833	18
1800–1815	16	1785–1799	15
1729–1784	50	1710–1728	19
1645–1709	81	1623–1644	22

It may appear that millisecond changes in the daily rotation of the solid earth would be of little consequence to fish populations. The connection is through energy exchanges, which can be quite large. Substantial changes in relative angular momentum of the global atmosphere are seen to occur on time scales of days to decades and longer. If the atmosphere gains or loses angular momentum (the propensity of a rotating object to remain in motion), then the earth must lose or gain the corresponding amount of energy (primarily angular momentum), which is seen as changes in the LOD. The importance of these changes is illustrated by the largest interannual variation in LOD on record of +0.5 ms as a consequence of the 1983 El Niño (Dickey et al. 1994). A change of similar magnitude was also noted for the 1997 El Niño event. The energy redistributions associated with the large 1983 El Niño resulted in the slowing of the rotation of the earth by 0.5 ms/day, which compares with decadal-scale changes in this century of about 4 ms (Fig. 3C), indicating that these decadal-scale changes in LOD represent large energy transfers.

The earliest estimates of the trends are approximations, as the error in the annual LOD estimates is relatively large (McCarthy and Babcock 1986). From 1800 until 1987, there were four periods of decreasing LOD, averaging 20.5 years in length and ranging from 15 to 32 years (Table 1). There were four periods of increasing LOD for this period, averaging 25.8 years and ranging from 16 to 38 years. From 1623 to 1799, we estimated there were three periods of decreasing trends, ranging from 15 to 22 years, and two periods of increasing trends of 50 and 81 years. A new trend of increasing LOD started in 1988. There are shorter periods of decreasing trends, such as from 1945 to 1948, that we have not distinguished as decadal-scale periods.

The LOD increased from 1950 to about 1972 (Fig. 3C). There was a brief interruption in the trend in the late 1950's and early 1960's, but in general, there was about a 2-ms in-

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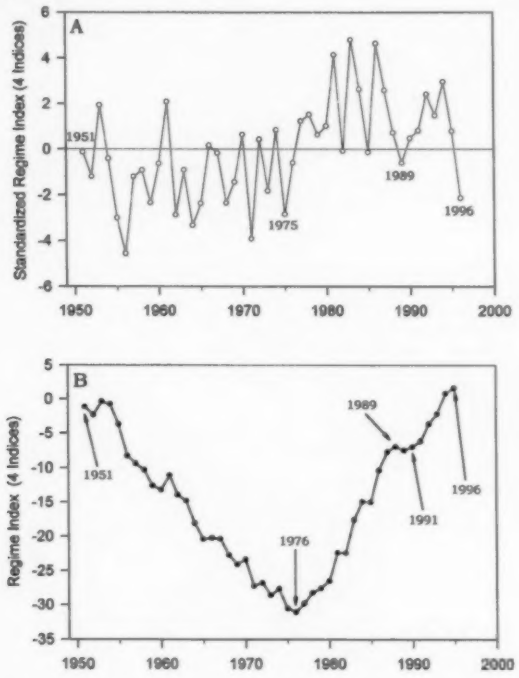
Fig. 4. (A) Sum of the standardized anomalies of the four pressure-related indices that form the regime index. (B) CuSum of Fig. 4A.



crease in the LOD. Beginning about 1973 or 1974, there was a speeding up of the solid earth that lasted until the late 1980's. A reversal in the trend is identifiable by 1989–1990 (Fig. 3C). Another change occurred in 1996 with the LOD decreasing substantially relative to 1995. An intervention analysis was conducted to test for changes in the mean level of LOD. Visually, changes were expected in 1972 and 1988 (Fig. 3C). LOD was found to be highly autocorrelated, and differencing was required prior to conducting the analysis. A plot of the differenced LOD data also suggested shifts in 1972 and 1988 given the persistent runs of positive and negative differences around each of these times. The intervention analysis did not yield significant changes at these times, however, likely due to the significant leverage (statistical) exerted by a few of the differenced data such as the large difference between the 1984 and 1983 observations.

Regime index

The six indices in our study were developed separately by investigators in different areas of science. As a result, the indices have different formats, but all indices have distinct trends that change in the mid-1970's. A simplistic measure of similarity would be to examine the correlation among the various indices. However, this single value (correlation) provides only a crude measure of similarity among the various indices. It does not provide information on the synchronous changes in the trend (mean level) such as the regime shift in 1976–1977. The synchronous change of all of the indices at about the same time provides relatively strong evidence of linked processes, particularly as the number of indices considered increases. Also, correlations reflect the measure of linear dependency between variables, and it is quite likely that any physical relationships may be nonlinear. These indices may also be more indicative of switches (binary or discrete) between or among regimes. In such cases, the relationship to salmon catch or abundance may be complex and (or) discontinuous. Relatively low correlations would be expected in such cases.

Pairwise correlations were calculated for each of the indices. These correlations were not intended to identify or quantify causal links (underlying physical mechanisms) or to construct dynamically linked (transfer function) models. Average correlations of $r = 0.60$ were found, with four being in excess of $r = 0.80$ (maximum $r = 0.88$). The weakest correlations ($0.2 < r < 0.3$) were found when NHST was compared with ALPI and ACI.

This similarity indicated that a combination of indices could be used to produce a composite index of regimes and regime shifts. We produced this composite index by dividing the annual anomaly of each of the four pressure-related indices (SOI, ALPI, NAOI, ACI) by the standard deviation of the time series and adding all standardized anomalies for each year. We reversed the signs of SOI, as it was opposite to the trends in the three other indices. The anomaly series for each index was estimated with a new series mean; thus the values may differ slightly from the anomaly values for the longer time series. The regime index (RI) is the CuSum of the sum of these standardized anomalies. The combined index (Fig. 4A) has distinct trends from 1951 to 1976 and changes abruptly in 1977, and the CuSum graph shows a distinct change in 1976 (Fig. 4B). The intervention analysis of the standardized anomalies for the RI identified significant changes ($P < 0.05$) in 1977 and 1989.

Other indices of regimes

The Pacific Interdecadal Oscillation (PDO) recently described by Mantua et al. (1997) identifies a pattern of decadal-scale variability in the North Pacific as the first principal component of sea surface temperatures (Fig. 5A). The oscillation is correlated with a variety of physical and biological systems including Pacific salmon production and discharge from large rivers on the west coast of North America. Zhang et al. (1997) and Minobe (1997) also identified shifts around 1942–1943 and 1976–1977, about the same years that PDO shifts. Remarkably, studies by Minobe (1997) and Zhang et al. (1997) identified identical regimes and timing of shifts to the PDO even though different approaches and different data sets were used. When we extend the ALPI CuSum back to 1899 and convert the PDO to a CuSum (Fig. 5B), we find that the regimes and years of change 1925, 1947, and 1977 are virtually identical in all indices except that we identify a change in 1989 that was not previously identified in the PDO (Mantua et al. 1997).

Interrelationships among climate indices and Pacific salmon and sardines

The periods of increased Pacific salmon production in this century occurred from the late 1920's to early 1940's and from the late 1970's to the mid-1990's (Fig. 6A). The ACI and all-nation catch of Pacific salmon follow the same general trend (Fig. 6B). There is also a strong correspondence

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Fig. 5. (A) Pacific Interdecadal Oscillation index (PDO) from Mantua et al. (1997). The PDO is the leading eigenvector values from principle components analysis of the North Pacific sea surface temperatures. (B) CuSum of Fig. 5A.

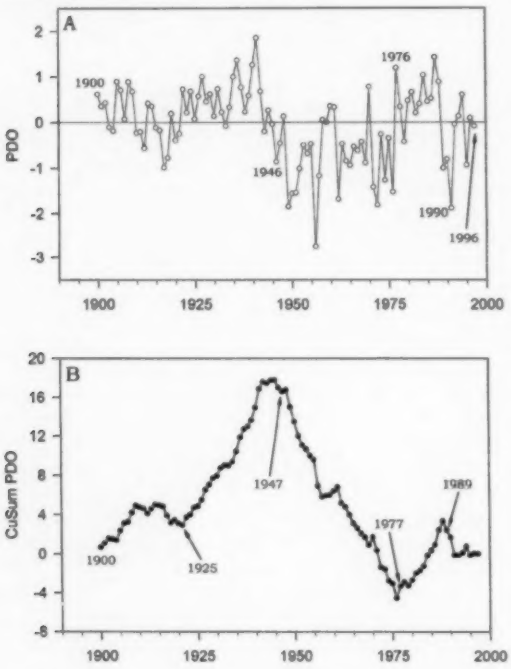
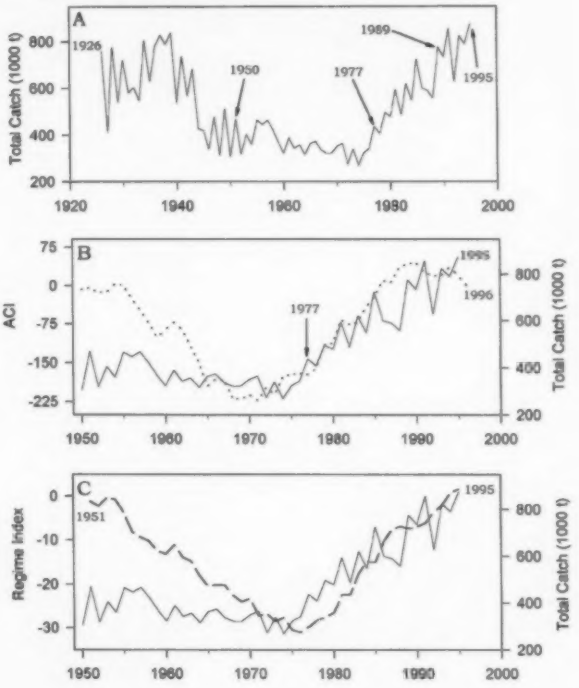


Fig. 6. (A) Total North Pacific catch of pink, chum, and sockeye salmon from 1926 to 1995. (B) Relationship between total catch (solid line) and general atmospheric circulation index (ACI) dotted line, from 1950 to 1995 (ACI is shown to 1996). (C) The relationship between total catch (solid line) and the regime index (broken line) from 1950 to 1995. Note that the CuSum form demonstrates the persistance of trends before and after the change in the late 1970's.



(r = 0.57) between all-nation salmon catch and our combined RI (Fig. 6C). A cross-correlation analysis was conducted to determine if ACI was related to salmon catch. The results indicated that including the ACI (lag 1) was useful in predicting salmon catch in the next year. A direct comparison is confounded by the life histories of the various salmon species in the catch. Nevertheless, it appears that changes in the Pacific salmon catch may lag the changes in the environment by 1 or more years, which may prove useful for estimating total salmon production in the North Pacific.

The periods of decreasing LOD in this century correspond to years of increasing Pacific salmon catch. It was not possible to develop an index of Pacific salmon abundance prior to the 1900's, but it is possible to compare the synchrony of abundance changes in three major sardine populations in the North and South Pacific oceans (Kondo 1986; Kawasaki 1991; Serra 1991) with the all-nation Pacific salmon catches (Figs. 7A–7D) and then compare the trends in catches of sardines off Japan (Fig. 7D) with the LOD time series (Fig. 7E). Not only are the fluctuations of salmon and sardines synchronous in this century, but the sardine populations off Japan and the Asian Far East, off Chile and the west coast of South America, and off California and the west coast of North America all fluctuated in abundance synchronously (Kawasaki 1991). Hiyama et al. (1995) showed that there was a dramatic decline in recruitment prior to the collapse of the Japanese sardine (*Sardinops melanostictus*), indicating that overfishing was not the cause.

Kondo (1986) summarized the catch records for the Japanese sardine fishery from the early 1600's until the present and concluded that there has been a history of extreme fluctuations in abundance. He identified alternating periods of good and poor catches starting in the 1650's. The periods of good catches from the early 1600's correspond closely (six out of seven periods) to the periods of decreasing LOD in Table 1 and to the two periods of increased Pacific salmon catches in this century (Figs. 7D and 7E). We identified one period of decreasing LOD from 1785 to 1799 that was not identified by Kondo (1986) as a period of possible good sardine catches. However, Ito (1961) identified a period of increased Japanese sardine production from about 1780 to 1850, and this would match the combined periods of decreasing rotation from 1785 to 1799 and from 1816 to 1833. Ito (1961) also identified a period of increased sardine production in the waters around Japan from 1550 to 1600, which is earlier than our LOD time series and slightly later than the increase in sardine scale deposits from about 1510 to 1540 off California (Baumgartner et al. 1992) (Table 2).

Baumgartner et al. (1992) identified periods of increased sardine scale deposition from about 1840 to 1880 and from 1900 to 1950, which correspond to the periods of decreasing LOD from 1859 to 1892 and from 1918 to 1934. The Baumgartner et al. (1992) data did not show large abundances of Pacific sardines (*Sardinops sagax*) in the early 1600's but do show that the abundance was high from 1670 to 1750, simi-

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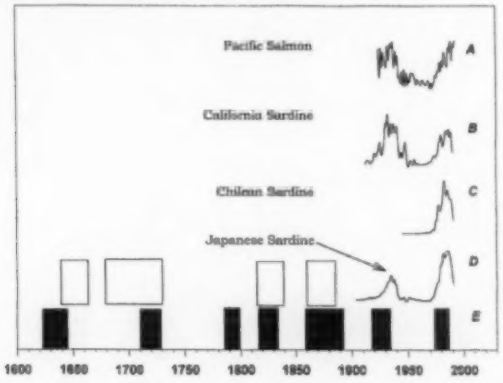
Fig. 7. Relationship among catches of Pacific sardines, total North Pacific catch of pink, chum, and sockeye salmon, and decreasing periods of length of day. (A) Pacific salmon. (B) Californian sardine scale is equivalent to 0 – 720 000 t at the maximum catch. (C) Chilean sardine scale is equivalent to 0 – 6 500 000 t at the maximum catch. (D) Japanese sardine scale is equivalent to 0 – 5 400 000 t at the maximum catch. Open rectangles show periods of high catches of Japanese sardines from 1640 to 1900. (E) Solid rectangles showing periods of decreasing trends in length of day.



lar to Japanese records (Kondo 1986). They do show that the abundance fluctuations were characteristic of the dynamics of the populations as far back as the year 360. Thus, in general, the periods of the good and poor catches of Japanese sardines match the periods of decreasing and increasing average annual LOD, respectively, and there is some similarity between strong and weak periods of California and Japanese sardine production.

Discussion

In our study, we show that there is a synchrony among major indices of climate in the Northern Hemisphere. The correspondence in trends is not exact, but there is a close similarity in the timing of changes. In some cases, evidence of synchrony is not new, such as the linkage between the Pacific and Atlantic pressure systems (Walker and Bliss 1932). Although we did not include the PDO (Mantua et al. 1997) in our regime index, the trends in the PDO were similar to trends in most of the indices we described, particularly when the PDO was shown in a CuSum form. The change we show in the late 1970's has been recognized in a number of other studies (e.g., Ebbesmeyer et al. 1991; Beamish 1993; Miller et al. 1994; Mantua et al. 1997). There is also a well-documented coherence between the changes in the trends of Pacific salmon catch and the change in the climate/ocean environment in 1976–1977 (Beamish and Bouillion 1993; Francis and Hare 1994; Hare and Francis 1995; Mantua et al. 1997). The synchrony of the responses among Pacific salmon, Pacific sardines, and the LOD is evidence that the shifts possibly occurred for centuries and before modern fisheries developed. This may indicate that Pacific salmon abundance may also have fluctuated naturally for centuries as a consequence of climate change.

The close relationship of the timing of the shifts among all of the indices of climate change indicates that a common event may precipitate these shifts. Variations in response lags are no doubt related to physical interactions between the atmosphere, oceans, and the rotation of the solid earth as well as to local and global oceanic processes. The complex interaction between the ocean and the atmosphere and the capacity for the ocean to integrate atmospheric changes resulting in lagged responses are one explanation for the variation in the response issues found in the indices. Steele (1998) noted that marine communities are more responsive to the types of changes we describe here than are communities on land.

Eubanks et al. (1986) and others showed a significant correlation between the LOD and the Southern Oscillation confirming the close relationship between interannual changes in the earth's atmosphere and LOD. Interannual fluctuations in LOD result largely from atmospheric forcing (Dickey et al. 1992). The decadal changes in LOD, which we associate with regimes, are generally attributed to core–mantle coupling (Hide et al. 1980; Lambeck 1980; Rosen and Salstein 1983), although an atmospheric contribution of 10–20% has been suggested (Lambeck 1980). Although interannual changes in LOD are generally assumed to be of meteorological origin, whereas decadal changes are generally attributed to core–mantle coupling, it appears that both the decadal and interannual changes in LOD are correlated with changes in climate indices on these time scales, suggesting that both have a common origin. Establishing the linkage between the decadal changes in LOD and the pattern of atmospheric circulation (e.g., Courtillot et al. 1982) may prove to be quite useful both in fisheries and ecosystem management.

Shifting regimes and changes in LOD may seem to be very far removed from the day to day problems of managing a particular salmon stock, but it does appear that these global systems are related to natural trends in fish production even for relatively small regions (Beamish et al. 1995). For fish populations, there is little doubt about the importance of water temperature. Additionally, Lambeck and Cavenaze (1976) have shown that since 1820 there appears to be a fair correlation between changes in the earth's rate of rotation and climate. Periods of acceleration appear to coincide with periods of warming and increased zonal winds, whereas periods of deceleration occur during periods of cooling and decreased zonal winds. Similarly, Fairbridge and Sanders (1987) identified accelerations of the earth with increased zonal circulation, mild winters in the Northern Hemisphere, and stronger monsoons in the tropics. A relationship between momentum changes of the earth's rotation and ocean processes has also been related to changes in the flow of the Gulf Stream (Mörner 1986). Thus, we believe that the LOD will become a useful index of environmental relationships when studying the dynamics of fish populations. Similarily, when the appropriate atmospheric circulation produces an increasing trend in the ACI, the resulting ocean circulation and upwelling pattern appear to be favorable for Pacific salmon production probably because of the intensification of the Aleutian Low (Brodeur and Ware 1992; Beamish and Bouillon 1993; Sugimoto et al. 1995).

The accumulating evidence of decadal-scale oscillations in the environment such as in the Baumgartner et al. (1992)

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Table 2. Historic records of sardine abundances off Japan and California in relation to years of decreasing length of day (LOD).

Decreasing LOD	Historic reports of large catches of sardines off Japan[a]	Periods of accumulation of sardine scales off California[b]
1973–1987		
1918–1934	1920–1945	1900–1950
1859–1892	1860–1885	1840–1870
1816–1833	1815–1840	1820–1840
1785–1799	No record of large catches[c]	
1710–1728	1680–1730	1670–1750
?–1644	1640–1665	No record of large catches
		1510–1540
		1330–1370
		1240–1280
		1150–1190
		915–1040
		680–705
		460–630
		360–400

[a]Estimated from fig. 1 in Kondo (1986).
[b]Years 360–1950 estimated from fig. 4 in Baumgartner et al. (1992).
[c]Ito (1961) identified 1780–1850 as a period of increased Japanese sardine production.

time series and in a number of other series such as those based on tree ring analyses supports the view that natural fluctuations have occurred for centuries. We stress that there is no reason to assume that shifts in regimes are cyclic, switching from one state to the opposite and back again. Thus, the change detected in our regime shift index in 1989–1990 does not have to be a switching back to pre-1977 conditions. For example, the weakening of the Aleutian Low after 1989 was associated with a dominant annual wind direction that was different from the dominant direction prior to 1977 as shown by the ACI and Fig. 5A. Similarly, we would expect that the weakening trend in ALPI since 1989 would be associated with changes in Pacific salmon production, but not necessarily a return to pre-1977 conditions. As the concept of regimes is developing, we expect that explanations for the differing responses between 1977 and 1989 will be identified and definitions will become more accurate. Our regime shift index (RI) is experimental and it remains to be seen if it is a useful way of classifying regimes and possibly of finding relationships that facilitate forecasting recruitment trends.

A strong relationship between fish population dynamics and climate emphasizes the need to understand the linkage between global warming (Kerr 1995) and fish population dynamics. The association of trends in surface temperatures (NHST) with both the RI and a number of the individual indices is evidence that the global warming time series is also influenced by mechanisms that determine regimes. In general, the concept of regimes and regime shifts stresses the need to improve our understanding of the mechanisms that regulate the dynamics of fish populations and their ecosystems.

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Perspectives on Canadian Marine Fisheries Management

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